PREDATORY HYMENOPTERAN ASSEMBLAGES IN BOREAL ALASKA: ASSOCIATIONS WITH FOREST COMPOSITION AND POST-FIRE SUCCESSION

By

Alexandria Wenninger, B.S.

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Biological Sciences

University of Alaska Fairbanks

MAY 2018

APPROVED:

Diane Wagner, Committee Chair
Teresa Hollingsworth, Committee Member
Derek Sikes, Committee Member
Kris Hundertmark, Chair
Department of Biology and Wildlife
Anupma Prakash, Interim Dean
College of Natural Science and Mathematics
Michael Castellini, *Dean of the Graduate School*

Abstract

Predatory Hymenoptera play key roles in terrestrial foodwebs and affect ecosystem processes, but their assemblage composition and distribution among forest habitats are poorly understood. Historically, the boreal forest of interior Alaska has been characterized by a fire disturbance regime that maintains vegetation composition dominated by black spruce forest. Climate-driven changes in the boreal fire regime have begun to increase the occurrence of hardwood species in the boreal forest, including trembling aspen and Alaska paper birch. Replacement of black spruce forests with aspen forests may influence predatory hymenopteran assemblages due to differences in prey availability and extrafloral nectar provisioning. Furthermore, changes in the frequency and extent of boreal forest fires increase the proportion of forests in earlier successional stages, altering habitat structure. The primary goal of this study was to characterize predatory hymenopteran assemblages in post-fire boreal forests of interior Alaska. To investigate this, the abundance, species richness, and composition of predatory hymenopteran assemblages were compared among forests at different stages of succession that were dominated by black spruce pre-fire, but that vary in their tree species composition post-fire. Predatory hymenopterans were separated into three groups: ants, macropterous wasps, and micropterous wasps. Ant species richness and abundance were not related to forest composition, but both were significantly higher in early-successional forests than in mid-late successional forests. In contrast, macropterous wasp morphospecies richness and abundance, as well as micropterous wasp abundance, were positively related to the basal area of aspen, suggesting that aspen forests benefit macropterous and micropterous wasps, perhaps due to extrafloral nectar provisioning and the availability of greater quality prey than is provided by black spruce. Wasp assemblages did not differ between successional stages. This study is the first to characterize the influence of post-fire succession on predatory hymenopteran assemblages of the boreal forest at a large spatial scale. The results suggest that continued

warming of the boreal forest will have cascading influences on the insect assemblages of boreal Alaska.

Table of Contents

List of Figures

Page

List of Tables

Page

List of Appendices

Page

Acknowledgments

I thank my major advisor, Diane Wagner (Associate Professor, Dept. Biology & Wildlife, UAF), for her unending support and expertise; I never would have made it this far without the countless hours we spent discussing how best to design, analyze, and present this research. I thank Derek Sikes (Associate Professor, Curator of Insects, Dept. Biology & Wildlife, UAF, University of Alaska Museum) for insightful conversation and curation of my beloved hymenopteran specimens into the University of Alaska Museum Insect Collection. I thank Teresa Hollingsworth (Research ecologist, UAF, USDA Forest Service, Boreal Ecology Cooperative Research Unit) for her insights into the vegetation communities of the boreal forest, and for her extensive data collection efforts across the Bonanza Creek Long Term Ecological Research sites. I thank the Bonanza Creek Long Term Ecological Research program (National Science Foundation) and site manager Jamie Hollingsworth for logistical support. I thank The HYM Course for teaching me the wasp identification skills necessary to conduct this work, and Bob Kula (Research Entomologist, USDA/ Systematic Entomology Laboratory) for his expertise and reassurances about the murky waters of morphospecies identification. I thank Ant Course for invaluable training in all things ants, and Rob Higgins (Assistant Professor, Thompson Rivers University, BC, Canada) for his insights on identification characters of boreal ants. This research was supported by grants from the Institute of Arctic Biology (Graduate Summer Research Award), the University of Alaska Fairbanks Ted McHenry Field Biology Research Fund, the University of Alaska Fairbanks College of Science and Mathematics (Travel grant), the University of Alaska Fairbanks Graduate School (Travel grant) and National Science Foundation DEB-1026415.

1 Introduction

Arthropods are exceptionally diverse and abundant and play vital roles in forest trophic structure and ecosystem function (Erwin 1982, Majer et al. 1994, Maleque et al. 2009). Despite their importance, the relationships between arthropods and habitat have been relatively understudied within the boreal forest (Danks and Foottit 1989, Bennett and Hobson 2009). In interior Alaska, the boreal forest undergoes regular fire intervals of approximately 100 years, and is characterized by stable, conifer self-replacement succession cycles, where deciduous broadleaf species characterize earlier stages of post-fire succession (Johnstone et al. 2010a). However, over the last century, boreal warming has reduced snowpack and thawed permafrost, which in turn has influenced the boreal fire regime by increasing forest fire frequency, severity, and extent (Wendler and Shulski 2009, Johnstone et al. 2010a, Johnstone et al. 2010b, Shenoy et al. 2011, Schuur et al. 2015). Climate-driven changes in the boreal fire regime have facilitated hardwood persistence, including trembling aspen (*Populus tremuloides*) and Alaska birch (*Betula neoalaskana*), in forests that were historically dominated by coniferous black spruce (*Picea mariana*) (Johnstone 2005, Johnstone and Kasischke 2005, Johnstone et al. 2010a, Lindroth and St Clair 2013). This increase in aspen in the boreal forest is of ecological interest, because aspen is highly palatable to herbivores and is one of few plants in the boreal forest that produces extrafloral nectar, both of which may influence arthropod community composition and trophic interactions (Heil 2015).

The foliage of hardwood species, such as aspen and birch, are poorly defended relative the foliage of coniferous species, such as black spruce (Bryant et al. 1983), and therefore may foster a robust prey base for predatory arthropods. In general, conifers tend to invest more in defensive compounds than hardwood species (Bryant et al. 1983), making them less preferred by generalist herbivores (MacLean and Jensen 1985, Baraza et al. 2006), which may reduce the diversity of prey available to predatory hymenopterans (Poelman et al. 2008). Less palatable

plants also suffer less leaf damage (Coley et al. 1985, Herms and Matson 1992), suggesting that they may generally provide fewer prey for predatory hymenopterans (Poelman et al. 2008). While surveys of insect diversity across broadleaf versus conifer habitats are limited, there is evidence that some insect taxa are more abundant and species-rich in aspen stands than in conifer stands (Hughes et al. 2000, Simonson et al. 2001). Less palatable plants also may alter the prey base if plant toxins are coopted as a defensive mechanism. Some herbivores consuming well-defended vegetation incorporate plant toxins into their bodies, reducing their quality as prey and the survivorship of their predators (Price et al. 1980, Ode 2006). These effects may be especially pronounced in parasitoids of herbivores, which develop within or alongside their hosts. The fitness of developing parasitoids may be impaired by plant chemical defenses either directly, through contact with toxins present in host tissues, or indirectly, through reduced host quality (e.g. reduced host body size, increased development time, and reduced host survivorship) (Ode 2006). Generalist parasitoids tend to experience a greater reduction in fitness than specialist parasitoids when exposed to plant defensive compounds (Sznajder and Harvey 2003, Ode 2006), and this may negatively influence parasitoid species diversity in stands of trees with strong chemical defenses. Therefore, we expect predatory hymenopteran abundance and richness to be low in black spruce stands relative to aspen and birch stands.

A second reason why forest composition is likely to influence predatory hymenopteran assemblages is that aspen produces extrafloral nectar, whereas birch and black spruce do not. Extrafloral nectar is a carbohydrate-rich solution secreted by nectaries that are typically located on a plant's leaves, stems, or bracts, rather than flowers (Bentley 1977, Koptur 2005). For many plant species, extrafloral nectar mediates an indirect plant defense by attracting and nourishing predatory hymenopterans such as ants and parasitoid wasps, which then may harass, consume, or parasitize herbivorous arthropods on the plant (Bentley 1977, Wäckers et al. 2005, Heil 2015). In general, access to extrafloral nectar improves the performance, longevity, and fecundity of parasitoid wasps and ants (Wanner et al. 2006, Byk and Del-Claro 2011, Jamont et

al. 2013). Because extrafloral nectar is an additional food source available to predatory hymenopterans, aspen stands may support a greater abundance of predatory hymenopterans than stands composed of other tree species. Additionally, the presence of a unique food source should provide additional niche space, which could increase the species richness of predatory hymenopterans (Gause 1934, Bluthgen and Feldhaar 2010). The influence of both extrafloral nectar and plant palatability may be especially pronounced in younger successional aspen stands for ants, because foliar resources, such as extrafloral nectar and foliar herbivorous prey, are more accessible to most ants on shorter, understory seedlings and saplings than on canopy-reaching trees. There are no arboreal-nesting ant species in boreal Alaska.

A third reason why predatory hymenopterans may associate with stands colonized post-fire by hardwood species in comparison to black spruce is that they share an association with the same microclimatic factors. Black spruce stands are typically characterized by cool, moist soils; these site are often underlain with permafrost, which prevents drainage, and the low rates of decomposition at these sites creates an accumulation of organic matter, which further retains site moisture (Johnstone et al. 2010a). High-severity fires favor recolonization of hardwood species in part because exposure of the mineral soil prohibits the regeneration of black spruce and reduces the soil's capacity to hold moisture (Johnstone et al. 2010a). Post-fire sites with shallow organic matter layers are associated with increased rates of aspen growth, decreased rate of black spruce growth, and warmer, drier soils than post-fire sites with deeper organic matter layers (Shenoy 2016), conditions which may also be preferred by predatory hymenopterans. Although studies are limited for wasps, warmer temperatures increase ant foraging and development rates (Finnegan 1973, Kipyatkov and Lopatina 2015), and water-logged soils tend to discourage ant nesting (MacKay et al. 1986). Because aspen and birch tend to grow in warmer, drier soils, there may be an association between predatory hymenopterans and hardwood species on the basis of environmental preferences.

Increases in forest fire frequency and extent will increase the area of boreal forest in younger successional stages. A forest's post-fire successional age may affect predatory hymenopteran assemblages largely due to its influence on microclimate and structural niche space. The open canopies of early-successional forests promote the growth of understory vegetation and allow insolation to warm the soil. As forests age, the canopy shades the understory, reducing the cover of understory vegetation and cooling the soil (Hart and Chen 2008, Chen and Robinson 2015). However, over time, leaf litter and dead wood accumulate, providing additional structure and insulation against cold temperatures (MacKinney 1929, Higgins and Lindgren 2006).

Studies of hymenopteran assemblages across successional time in other ecosystems have produced conflicting results. In temperate and sub-boreal conifer forests, ant abundance and species richness decrease over successional time post-logging (Palladini et al. 2007, Higgins and Lindgren 2015). However, similar research conducted in the tropics has shown that ant richness is highest in mature forests, due to a large number of species dwelling in leaf litter (Silva et al. 2007). A study in subtropical China found that ant abundance and richness are unrelated to successional age; however, the assemblage composition of ants differed between young and old successional forests (Staab et al. 2014). Because boreal Alaska has no known litter-dwelling ant species, early-successional forests likely benefit ant abundance and species richness, due to the reduced canopy cover and warmer soil temperatures (Chen and Robinson 2015). Unfortunately the assemblage patterns of wasps over successional time are even less well known than those of ants. In broadleaf forests of Japan, parasitoids of herbivores decrease in abundance over successional time, as understory vegetation is shaded by taller, woody species; however, parasitoids of detritivores increase in abundance over successional time as leaf-litter mass increases (Maleque et al. 2010). Evidence from temperate forests suggests that the overstory supports higher abundances of predatory and parasitoid wasps, as well as increased parasitism rates, relative to the understory (Sobek et al. 2009), suggesting that

forests in later successional stages may support greater abundances of wasps than earlier successional forests. In boreal Alaska, the structural complexity and buildup of organic matter in more mature successional forests may support more abundant and species-rich assemblages of wasps.

The primary goal of this study was to characterize predatory hymenopteran assemblages in post-fire boreal forests of interior Alaska. We hypothesized that aspen stands would support a greater abundance and richness of predatory hymenopterans relative to birch or black spruce stands. We also hypothesized that differences in forest structure between earlier and later successional stages would affect predator hymenopteran assemblages. In particular, ant species richness and abundance may decline over time, whereas wasps may increase in species richness and abundance over time. To test this, we characterized associations between predatory hymenopteran abundance, species richness, and assemblage composition in forests that vary in their tree species composition and time since last burn. Because of differences in mobility and use of resources, these relationships with boreal forest habitats are explored for ants and wasps separately.

2 Methods

2.1 Study sites.

We sampled 29 study sites from the Bonanza Creek (BNZ) Long Term Ecological Research (LTER) regional site network (RSN) based on their age and current forest composition (Table 1). The study sites were located along major road systems within a 2.3 million ha area of interior Alaska centered around Fairbanks, AK (Figure 1). Each study site covered 1200 m^2 (30 m x 40 m). Sites were characterized by the BNZ LTER as “young,” “intermediate,” or “mature” age class based on the date of the last burn. A total of 13 young

sites were sampled, of which 7 resulted from the Dall City fires (burned in 2004) and 6 from the Boundary fire (2004). The 12 intermediate sites sampled consisted of 6 sites from the Gerstle River fire (1947), 3 sites from the Murphy Dome fire (1958), 1 site from the Goldstream fire (1966), and 2 sites from the Wickersham Dome fire (1971) (Table 1). The four mature sites burned prior to available records, but likely burned as the result of four separate fires. Common tree species at these sites include black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg), trembling aspen (*Populus tremuloides* Michx), and Alaska birch (*Betula neoalaskana* Sarg.); less common species include white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch), and balsam poplar (*Populus balsamifera* L.). All tree species were identified by the Bonanza Creek LTER. Prior to the most recent burn, all sites were dominated by black spruce forest; however, the forests that have regenerated since the most recent fire vary in their aspen, birch, and black spruce compositions. The study sites include both aspen-abundant and aspen-poor forest compositions within each age class except mature. The BNZ LTER RSN only contains mature black spruce sites, because sites were chosen with the purpose of understanding changes that may occur in the "typical" boreal black spruce relay succession, and hardwood persistence is a relatively recent phenomena in boreal Alaska (Teresa Hollingsworth, U.S. Forest Service, University of Alaska Fairbanks, personal communication May 2017).

Table 1: List of 29 LTER RSN study sites with their associated age class, burn year, and location information (WGS84 datum).

Site ID	LTER Age Class	Burn Year	Latitude	Longitude
MD2	Intermediate	1958	64.8827	-148.3555
MD5	Intermediate	1958	64.8791	-148.3815
MD8	Intermediate	1958	64.8829	-148.3982
WD6	Intermediate	1971	65.1453	-148.0189
WD8	Intermediate	1971	65.1487	-148.0264
GS2	Intermediate	1966	64.8026	-148.4204
GR1	Intermediate	1947	63.7913	-145.0419
GR2	Intermediate	1947	63.7876	-145.0553
GR3	Intermediate	1947	63.8004	-145.0556
GR4	Intermediate	1947	63.8018	-145.0614
GR5	Intermediate	1947	63.7950	-145.0766
GR9	Intermediate	1947	63.7721	-145.0792
DC39	Young	2004	66.1686	-150.2018
DC40	Young	2004	66.1637	-150.2029
DC42	Young	2004	66.1517	-150.1803
DC44	Young	2004	66.1407	-150.1711
DC51	Young	2004	66.0745	-150.1679
DC53	Young	2004	66.0721	-150.1673
DC54	Young	2004	65.9103	-149.7803
BF61	Young	2004	65.3494	-146.6681
BF63	Young	2004	65.3528	-146.6747
BF76	Young	2004	65.1234	-147.4654
BF78	Young	2004	65.1530	-147.4812
BF79	Young	2004	65.1509	-147.4762
BF84	Young	2004	65.1535	-147.4781
GSM2	Mature	1804-1843	64.8033	-148.3157
UP4C	Mature	"pre-1930"	65.1539	-147.4913
NRM2	Mature	"pre-1930"	64.6833	-148.5599
TRM4	Mature	1844-1902	65.4100	-148.2318

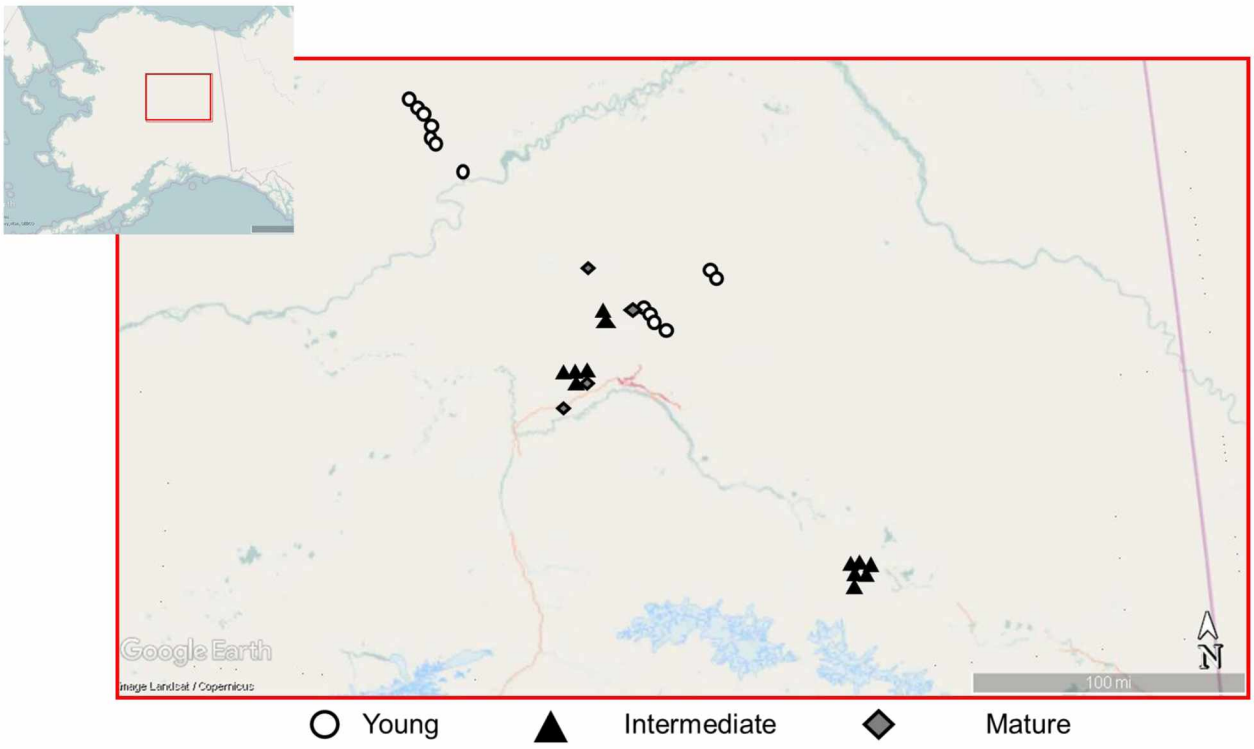

Figure 1: Map of 29 LTER RSN study sites located throughout interior Alaska. Each site is represented by a point, indicating its LTER age classification (see text for definitions for these categories).

2.2 Predatory hymenopteran collection.

To assess predatory hymenopteran species richness, abundance, and assemblage composition, arthropods were sampled three times at each site during the growing season using two methods. Arthropods were sampled from the ground surface with pitfall traps. At each site and sampling period, 12 pitfall traps were placed at 10 m intervals within a 20 m by 30 m grid (total of 36 pitfall traps per site). Pitfall traps were constructed from 200 mL cups with a 6 cm diameter opening containing approximately 75 mL of a pre-diluted propylene glycol solution (20% propylene glycol, 20% glycerin, 60% deionized water: Splash brand RV & Marine Antifreeze). A pinch of bittering agent (denatonium benzoate) was added to discourage bear interest. Each pitfall trap was placed in the soil so that the upper edge of the trap was flush with the ground surface, and a foam plate was suspended 3 cm above the trap to prevent rain water

from entering and overflowing the trap. Pitfall traps remained in the field for seven days per sampling period. In order to capture variation in assemblages across the growing season, each site was sampled once in each of the months of June, July, and August in 2014 and/or 2015. Samples were stored in the propylene glycol solution until processed, at which point they were temporarily stored in 95% ethyl alcohol until identification processing.

Predatory hymenopterans were also sampled from vegetation via sweep netting. Sweep sampling took place once during each pitfall-sampling period (total of three sweep samples per site), on the same day as pitfall trap placement unless it was raining, in which case sweep sampling was delayed until pitfall collection seven days later. Sweep sampling consisted of 100 sweeps per site. Upon collection, the contents of the sweep net were deposited in a one-gallon Ziploc bag for temporary storage. Samples were frozen for at least 24 hours before being transferred to vials of 95% ethyl alcohol where they remained until identification processing.

2.3 Predatory hymenopteran identification.

Ants were identified to the species level using a variety of published sources (Francoeur 1997, Ellison et al. 2012, Glasier et al. 2013, AntWeb 2014), personal communications with Dr. Rob Higgins (Thompson Rivers University, BC, Canada, 2014-2016), and by comparison to museum specimens at the University of Alaska Museum Insect Collection. Once identified, ants were either point-mounted as part of a voucher collection for the UA Museum or preserved in 95% ethyl alcohol for long-term storage. The ant species identified as *Leptothorax muscorum* likely represents a group of cryptic species, and is more appropriately considered a species complex (Philip S. Ward, University of California Davis, personal communication 7 August 2015). For simplicity, we simply refer to this species complex as "*Leptothorax muscorum*".

Wasps were pin or card-mounted depending on size and identified to the lowest taxonomic level possible using Goulet and Huber (1993). The same source was used to

determine the known feeding habits of each taxonomic group of wasps, in order to validate that wasp taxa were predators or parasitoids during one or more stages of their lives. Wasps were grouped based on morphology into presumed species (hereafter "morphospecies"). Morphological characteristics used to define morphospecies included, but were not limited to: color, shape, size, pubescence, texture, or articulation, of the body (mesosoma/metasoma), wings, antennae, face, eyes, legs, or mouthparts. When possible, male wasps were given the same morphospecies identification as their respective female wasps; however, if male wasps were too morphologically dissimilar to associate with a female wasp, then they were excluded from analyses to avoid overestimating morphospecies richness. Additionally, a few wasp specimens that were too damaged to accurately identify were also excluded from analyses. Hymenopteran voucher specimens were donated to the University of Alaska Museum Insect Collection for long-term preservation (accession number: UAM-2017.10-Wenninger-Ento).

2.4 Forest characteristics

To assess tree species composition and structure, the overstory and understory basal area of each tree species (m^2/ha) was quantified at each site. As per BNZ LTER specifications (as used in Hollingsworth et al. (2010)), overstory trees were defined as individuals with a diameter at breast height (dbh) of at least 2.5 cm (breast height=1.37 m). For overstory trees, the dbh was used to calculate basal area. Understory individuals were defined as all tree seedlings and saplings with a dbh smaller than 2.5 cm or a total height shorter than 1.37 m. For these smaller individuals, basal area was estimated from the diameter at the base of the stem. At the intermediate sites, every overstory tree dbh was measured in 2013 by the BNZ LTER (Van Cleve et al. 2015). Understory seedlings/saplings at all sites, and overstory trees at the young sites, were all measured via transect, and these basal areas were used to estimate basal area across the entire site. Two 2-m wide transects were surveyed at each site, along the length

(30 m) of each site on two sides (intermediate sites: 220 m^2 of transect sampled in 2013 by BNZ LTER; young sites: 120 m^2 of transect sampled between 2015 and 2016 by BNZ LTER and A. Wenninger) (Hollingsworth 2015).

2.5 Environmental variables.

Environmental variables assessed at each site included slope, aspect, elevation, percent canopy cover, soil moisture potential, and soil temperature (mean and minimum). Slope (degrees), aspect (degrees, corrected for declination), and elevation (m) were retrieved from the "Bonanza Creek LTER Data Catalog" (Bonanza Creek LTER 2014) (Johnstone and Hollingsworth 2013).

Percent canopy cover was assessed by taking four measurements (one in each of four cardinal directions) at each of six random locations within each plot using a convex spherical densiometer in 2014 or 2015. Measurements were taken between August and October. The four measurements at each location were averaged to get a single percent canopy cover for that location. All six locations were then averaged across the site.

Each site was characterized by its soil moisture potential and soil temperature. Soil moisture potential was categorized on a scale ranging from xeric (dry, category one) to subhygric (wet, category six) based on site topography, permafrost extent, and soil texture (Johnstone et al. 2008). Young sites were assessed in 2008, intermediate sites in 2011, and mature in 2001 by BNZ LTER. Because the factors affecting potential moisture are relatively slow to change, the BNZ LTER data were still considered relevant, despite the time passed since the last measurements were taken. To assess soil temperature, three "smartbutton" temperature sensors were deployed per site, enclosed in 20 mL Nalgene containers to protect from water damage. Sensors were dispersed across the site, approximately 20 m apart, and buried 10 cm below the ground surface. Temperature sensors were programmed to record the

temperature once every four hours at each site starting with the first recording at 1800 h on 3 June 2015 to the last recording at 1400 h on 11 September 2015. Mean growing season temperature was calculated as the average temperature recorded across all three sensors per site. A minimum temperature value was calculated by averaging the lowest temperature recorded by each of the three sensors at a site. One mature site was excluded from all soil temperature analyses, because local wildlife continued to displace the sensors throughout the growing season.

2.6 Data analysis: calculation of predatory hymenopteran assemblage metrics.

Predatory hymenopteran assemblages were characterized by species (or morphospecies) richness, abundance, and, for ants only, biomass. Data collected from pitfall and sweep sampling methods were combined at each site across all three sampling periods. Ants were analyzed separately from wasps. Furthermore, we distinguished between wasp taxa that were likely volant and had access to aboveground plant resources, such as extrafloral nectar and foliar herbivorous prey, and predominantly litter-dwelling adapted taxa with reduced flight capabilities, which were unlikely to access foliar resources. Wasps were categorized as "macropterous": taxa with fully developed wings that reach at least as far as the posterior end of the metasoma, or "micropterous": apterous and brachypterous taxa.

Because ants live in colonies, it cannot be assumed that individual pitfall captures of ants were independent events. For instance, nests that were closer to pitfall traps may have inflated the estimate of abundance if many ants fell in that trap simply due to its proximity to the nest; a nest of the same size farther from the pitfall trap at a site may have collected relatively fewer ants (Gotelli et al. 2011). To adjust for this, the ant abundance from pitfall traps was calculated on a sample basis, where the abundance was based on the number of traps that ants of each species were caught in at a site, rather than the raw number of individual ants caught in

those traps (Longino et al. 2002, Gotelli et al. 2011). Ant abundance values at each site were calculated using this occurrence-based method, which better approximates colony abundance.

Ant biomass (mg) was estimated at each site by multiplying the total number of ants at a site of each species by the average dry weight of a worker of that species. The average species worker weight was obtained from the dry biomass of 10 individuals per species. Ants were dried for 5 days in a drying oven set to 60 °C. Ant biomass was reported as the dry mass of ants (mg) per m^2 area sampled across all three sampling periods.

2.7 Data analysis: rarefaction and species accumulation curves

While the intent of this study was to characterize the species richness of ants, macropterous wasps, and micropterous wasps among sites that vary in forest composition and successional age based on equal sampling effort, the total species richness of these taxa is also of interest, especially with regard to the more poorly studied micropterous wasps. To assess the thoroughness with which we sampled the species richness of ants, macropterous wasps, and micropterous wasps present in this study area as a whole, we assessed the accumulation of species collected over our sampling units. To create species accumulation curves, we plotted the sample-based rarefied species richness as calculated by the program Estimate S (version 9.1) against the number of sites sampled (each site represents a sample unit) (Gotelli and Colwell 2001). Curves that reach an asymptote were interpreted to indicate that all species that occur in the area were likely sampled, and curves that did not reach an asymptote were interpreted to mean that there are likely species present at the sites that were not sampled in this study.

2.8 Data analysis: addressing spatial autocorrelation.

Ideally, sites characterized by differences in successional age and forest composition would be spatially interspersed; however, this was not practical due to logistic constraints. Much of interior Alaska is inaccessible due to limited roadways and boggy or mountainous terrain with communication services limited to satellite phone or messaging. Accessible areas are limited by LTER land-use permissibility, and we further limited chosen sites to the LTER's intensive sampling network (an extent of approximately 2.3 million ha). These sites had background data available and are regularly sampled by the LTER, unlike their broader, extensive network (7 million ha extent). Site choice was limited to those encompassed by the LTER network because we felt it prudent to contribute data to the LTER site network, both to support advances in long-term understanding of the boreal forest arthropod communities, and so that future researchers may most effectively benefit from the data collected. With these constraints in mind, we chose the most informative sites for the study design. When we compared the percent of basal area composed of each aspen, birch, and black spruce by latitude, there was no change in tree species composition across latitude ($F_{1,27} \leq 0.13$, $p \geq 0.717$). Furthermore, there was no change in forest composition across elevation ($F_{1,27} \leq 01.42$, $p \geq 0.244$). However, there was some spatial aggregation of sites within age classes. Young sites accessible to sampling occurred at a higher mean latitude than the intermediate-aged sites (one-way ANOVA – $F_{2,26} = 19.6$, $p = <0.0001$) (Table 2A). The intermediate sites occurred at somewhat higher elevation than the young sites, though statistically this difference was not significant (one-way ANOVA – $F_{2,26} = 1.41$, $p = 0.263$) (Table 2B). Due to multicollinearity, latitude and elevation could not be included with successional age as independent variables in data analyses. However, other methods were employed to better understand the influence of spatial autocorrelation on the results.

Table 2: Summary of the latitudinal (A) and elevational (B) characteristics of sites belonging to young, intermediate, and mature age classes.

A) Latitude (°N)	Age class		
	Young	Intermediate	Mature
Mean	65.68959	64.37413	65.01263
Standard error	0.12983	0.17814	0.16586
Minimum	65.1234	63.77212	64.68328
Maximum	66.16865	65.14868	65.40996
B) Elevation (m)	**Age class**		
	Young	Intermediate	Mature
Mean	316	410	270
Standard error	53	46	73
Minimum	135	129	163
Maximum	770	575	485

The aggregation of sites within age classes complicates the investigation of forest-related effects on predatory hymenopteran communities in two ways. First, due to spatial autocorrelation, environmental conditions that characterize the areas sampled might differ from the larger, regional set of habitats of similar age within interior Alaska, which could influence the hymenopteran community through bottom-up processes. To investigate this, the environmental characteristics of the sampled sites were compared to the broader set of all LTER RSN sites within young (n = 90 sites) and intermediate (n = 31 sites) forest age classes that extend across approximately 7 million ha of interior Alaska using a permuted subsampling test (Politis and Romano 1994). Environmental variables tested included slope, aspect, soil moisture potential, and soil organic layer depth. For each variable and age class, a distribution of 1000 simulated means was constructed, each generated by randomly drawing without replacement a representative set of values (13 for young, 12 for intermediate). A *p*-value was calculated as the number of simulated means at least as extreme as the mean of the study sites, divided by the total number of simulations run (1000) ($\alpha = 0.05$). Second, although we expected forest composition and successional age to exert strong controls over predatory hymenopteran assemblages, it is possible that any patterns detected might actually be driven by underlying

environmental factors associated with latitude and elevation. To explore this, correlations (Pearson's *r*) were tested between the spatial variables (site latitude and elevation) and several environmental variables likely to vary across these gradients: slope, aspect, soil moisture potential, and mean and minimum soil temperatures. If environmental variables followed patterns commonly associated with global climatic gradients, sites at higher latitudes and elevations would be expected to be cooler and more arid. Strengths of correlations were assessed using the guidelines outlined by Cohen (1992), where strong, moderate, and weak correlations correspond to magnitudes of Pearson's $r \geq 0.5$, $0.5 > r \geq 0.3$, and $0.3 > r \geq 0.1$, respectively. Magnitudes of $r < 0.1$ are considered non-correlated. Studies of ant diversity along geographical gradients have generally shown that ant species richness decreases as latitude and elevation increase (Kusnezov 1957, Janzen and Pond 1975, Cushman et al. 1993). The negative relationship between ant species richness and increasing latitude and elevation is largely influenced by temperature, wherein the cooler temperatures of high elevations act as an environmental filter, limiting ant species richness (Sanders et al. 2007, Machac et al. 2011). Relationships between wasps and spatial gradients within the published literature were less clear, largely due to limited research. There is some evidence of declines in parasitic wasp diversity at high latitudes and altitudes (Noyes 1989); however, other research reported no difference in wasp species richness across latitudes or elevations (Janzen and Pond 1975). Overall, it appears that the species richness of both ants and wasps tends to decline with increasing latitude and elevation, though ants may respond more strongly to spatial gradients than wasps. In this study, because young sites tended to occur north of intermediate-aged sites, the expected latitudinal trend of reduced species richness at higher latitudes runs counter to the expectation that predatory hymenopteran richness will decline as post-fire succession proceeds in time, providing a conservative test of the hypothesis.

2.9 Data analysis: predatory hymenopterans and their relationship to forest composition.

To assess relationships between predatory hymenopteran assemblages and forest characteristics, a multimodel inference approach was employed to describe relationships between assemblage richness and abundance for ants, macropterous wasps, and micropterous wasps and understory/overstory basal areas of three tree species common to the study sites: aspen, birch, and black spruce. For the multimodel inference method of describing how predatory hymenopterans were associated with forest characteristics, we assessed how overstory and understory basal areas of aspen, birch, and black spruce relate to the predatory hymenopteran assemblage metrics (richness and abundance of ants, macropterous wasps, and micropterous wasps, as well as ant biomass) using model selection of multiple regression (multimodel inference) (Burnham and Anderson 2002). All assemblage metrics were calculated from combined pitfall and sweep data within sites. All multimodel inferential analyses were performed in RStudio version 1.0.136, R version 3.3.3. Before conducting model selection, a full model of all forest predictor variables (basal areas of aspen understory, aspen overstory, birch understory, birch overstory, black spruce understory, and black spruce overstory) was first run for each hymenopteran assemblage metric, and this full model was used to verify that the data meet the assumptions of linear multiple regression (function: lm, package: stats version 3.3.3). Linearity was assessed by visually inspecting plots comparing each predictor with the response variables. Normality was assessed by visually inspecting the normal probability plot of the standardized residuals of the full model. Equal variance was assessed by visual inspection of the residuals versus fits plot of the full model and by both Breusch-Pagan (function: bptest, package: lmtest version 0.9-35) and non-constant variance score tests (function: ncvTest, package: car version 2.1-4) (α=0.05). Ultimately, to meet the multiple regression assumptions ant richness, abundance, and biomass were natural-logarithm transformed, and micropterous and macropterous wasp abundances were square-root transformed. Once the models met the

assumptions of the test within reason, multicollinearity among predictor variables was checked by calculating the variance inflation factors (VIF) (function: vif, package: car version 2.1-4), imposing the cutoff of desiring an average VIF of less than 2 and no single variable VIF greater than 10. The average VIF of our predictor variables was 1.59, and no single variable VIF exceeded a value of 2, suggesting that multicollinearity was not an issue among our predictor variables.

Model selection was performed on each predatory hymenopteran assemblage metric by use of an all-subsets routine, ranking all 64 possible models (every combination of the 6 forest predictor variables, plus the null model which includes only an intercept) in descending order by weighted AICc (Akaike Information Criterion, corrected for small sample sizes) (function: dredge, package: MuMIn version 1.15.6). A confidence set of models was selected from the full set of models by descending through the AICc weight-ranked models, retaining all models in which the AICc weights cumulatively summed to ≤ 0.95 (Burnham and Anderson 2002, Symonds and Moussalli 2011). From this confidence set, model-averaged parameter coefficients were derived, weighted by AICc, and these parameters were accompanied by adjusted standard errors and confidence intervals, to obtain a sense of the variability around the estimated parameter while correcting for small sample sizes (function: model.avg, package: MuMIn version 1.15.6). The conditional parameter coefficients were referred to, meaning that the coefficients were averaged only across models that included that predictor. The conditional coefficients were more appropriate because the goal was to determine how predatory hymenopterans were related to tree species and structure, rather than using all the coefficients together to predict predatory hymenopteran abundance, species richness, etc. (Symonds and Moussalli 2011). 85% confidence intervals were reported because it has been shown that 85% confidence intervals are more appropriate under this multimodel inferential framework (Arnold 2010) (function: confint, package: MuMIn version 1.15.6). The direction of the relationships was confident for parameters in which the 85% confidence intervals do not overlap zero, and the

importance of these parameters was corroborated by comparing to the relative importance values (Burnham and Anderson 2002). The relative importance of each predictor variable on each response variable was determined by summing the weighted AICc values of all the confidence models in which that the predictor appeared (Burnham and Anderson 2002) (function: model.avg, package: MuMIn version 1.15.6).

The model averaged parameter coefficients with standard errors and confidence intervals, as well as the relative importance of parameters, were used to determine strengths of relationships between forest characteristics and predatory hymenopteran metrics. AICc ranks models based on their quality relative to one another, however, it does not assess whether the models it ranks are actually effective at explaining the response variable (Symonds and Moussalli 2011). To assess overall model fit, we report R^2, adjusted R^2, F statistic (assesses whether the model as a whole outperforms an intercept-only model, or whether the model explains more than random variance), and Cohen's f^2 measure of effect size (based on the adjusted R^2 value) for each full model of predatory hymenopteran assemblage metrics. Because the model selection procedure was based on all subsets of this full model, we were confident that models that fit well overall would also fit well when reduced to a candidate set (Symonds and Moussalli 2011). To assess Cohen's f^2, the following guidelines for effect size were used: $f^2 = 0.02$: weak effect, $f^2 = 0.15$: moderate effect, $f^2 = 0.35$: strong effect (Cohen 1992). Models with larger effect sizes were better able to explain predatory hymenopteran metrics by forest characteristics.

2.10 Data analysis: predatory hymenopterans and their relationship to successional age.

To test hypotheses addressing predatory hymenopteran assemblage patterns among forest habitats in different successional stages, mean metrics of predatory hymenopteran assemblages were compared across predefined categories of successional age using two-

sample *t*-tests. Sites were assigned by age as “early” or “mid-late” successional based on the time since the last burn. Sites that the BNZ LTER considers young (< 15 years since fire) were categorized as “early-successional” (N = 13). Because there were only four mature sites included in this study, all sites considered intermediate or mature (> 40 years since fire) by the BNZ LTER were categorized as "mid-late successional" (N = 16). Two-sample *t*-tests were used to test for mean differences in ant, macropterous wasp, and micropterous wasp species (or morphospecies) richnesses and abundances, as well as ant biomass, between successional age categories (early vs. mid-late) ($\alpha = 0.05$). Predatory hymenopteran metrics were transformed in the same way as they were for the multimodel analysis prior to the two-sample *t*-test analysis to meet the assumptions of equal variance and normality. All two-sample *t*-tests were performed in JMP Pro version 11.2.1.

2.11 Data analysis: predatory hymenopteran assemblage composition.

To compare the composition of predatory hymenopteran assemblages among forest characteristics we used multi-response permutation procedures (MRPP) (Mielke 1984). MRPP is a non-parametric method of assessing differences in composition among groups (McCune and Grace 2002), and for our purposes, tested differences in hymenopteran assemblage composition (both presence of a species and the abundance of that species) among sites of different successional ages and forest compositions. Successional age categories were defined in the same way as above for the two-sample *t*-test analysis. To categorize tree species composition, all sites were categorized by the dominance of aspen. Sites containing >50% basal area of aspen were classified as aspen-dominated, hereafter “aspen”, and those containing <50% aspen were classified as non-aspen dominated, hereafter “non-aspen”. (All aspen sites were actually composed of >60% basal area of aspen). This created four categories: early-successional aspen, early-successional non-aspen, mid-late successional

aspen, and mid-late successional non-aspen (sample sizes 4, 9, 7, 9, respectively). This procedure was conducted separately for ants, macropterous wasps, and micropterous wasps. Sørensen (Bray-Curtis) distance was used to measure differences among groups, because it is less influenced by outliers (McCune and Grace 2002). The test statistic, *T*, measured the separation among groups, where more negative values represented greater separation. The test also assessed the variable *A*, a metric of agreement within groups with a maximum of 1, where an $A > 0$ signifies that there was less heterogeneity within groups than would be expected by chance. *A* also serves as a measure of effect size. Pairwise comparisons among categories were conducted if the overall *p*-value was <0.10. To assess whether assemblage composition was driven by forest characteristics such as successional age and species composition, pairwise comparisons were made between early-successional groups, mid-late successional groups, aspen groups, and non-aspen groups, for a total of four pairwise comparisons which were corrected for multiple comparisons using a serial Bonferroni adjustment, also called the Holm method (Holm 1979) (family-wise $\alpha = 0.05$).

Relationships among particular ant species and forest categories were assessed using indicator species analysis (ISA), which assesses the specificity of a species to habitat types based on exclusivity, the degree to which a species is *only* found in that habitat type, and faithfulness, the degree to which it is *always* found in that habitat type. Indicator values (IV) range from 0 to 100, with 100 signifying perfect indication, meaning the species is only and always found in that habitat type (Dufrene and Legendre 1997). Statistical significance of indicator values are assessed by comparing the observed IV with the mean IV from 4999 permutations of a Monte-Carlo random reassignment of species to habitat types. Here, the ISA assessed each species' specificity to forest composition and successional age categories ($\alpha = 0.05$). The ISA was not performed for macropterous or micropterous wasps because we collected too few individuals of most wasp species to conduct the analysis due to high species richness. Furthermore, without a scientific name attached to the morphospecies label, it would

be difficult for others to use and benefit from this information. All non-parametric analyses were performed in PC-ORD version 6.21.

2.12 Data analysis: predatory hymenopterans and their relationships with environmental variables.

To explore the relationships between local environmental variability and predatory hymenopteran assemblages, we examined correlations between predatory hymenopteran assemblage metrics and key environmental variables. Predatory hymenopteran assemblage metrics include ant, macropterous wasp, and micropterous wasp richnesses and abundances, and for ants, biomass as well. To address the influence of soil microclimate on predatory hymenopteran assemblages, we used three variables: soil moisture potential, mean soil temperature, and minimum soil temperature. Both mean and minimum soil temperatures were explored because in some areas of boreal Alaska, temperatures may reach critical minimums for thermophilic species, such as ants (Higgins 2010). We also included site slope and percent canopy cover variables, due to their indirect influences on temperature and leaf litter deposition. To whether predatory hymenopterans may associate with aspen on the basis of shared environmental preferences, soil moisture and temperature were correlated to the relative basal area of aspen (Pearson's r). Strengths of correlations (Pearson's r) were assigned using the guidelines outlined by Cohen (1992), where strong, moderate, and weak correlations correspond to magnitudes of Pearson's $r \geq 0.5$, $0.5 > r \geq 0.3$, and $0.3 > r \geq 0.1$, respectively. Magnitudes of $r < 0.1$ are considered non-correlated. All correlations were performed in JMP Pro version 11.2.1.

3 Results

3.1 Predatory hymenopteran assemblage description.

Pitfall trapping and sweep netting collected a total of 2659 ant individuals (1043 discrete occurrences) of a total of seven species: *Camponotus herculeanus* (Linneaus), *Myrmica alaskensis* (Wheeler), *Leptothorax muscorum* (Nylander), *Formica neorufibarbis* (Emery), *F. subaenescens* (Emery), *F. aserva* (Forel), and *F. podzolica* (Francoeur). Most ant captures occurred in pitfall traps (Table 3). All species of ant were captured from both collection methods except *Formica aserva*, which was absent from sweep net samples. The dry biomass of an average worker individual of each ant species, which was used in the calculation of overall ant biomass, is summarized in Appendix A, Table A-1.

A total of 1176 wasp individuals were collected, 1092 of which were grouped into 363 morphospecies belonging to nine superfamilies: Cerphronoidea, Chalcidoidea, Chrysidoidea, Cynipoidea, Diaprioidea, Ichneumonoidea, Platygastroidea, Proctotrupoidea, and Vespoidea. Of the wasps categorized to morphospecies, 853 individuals (326 morphospecies) were characterized macropterous and 239 individuals (37 morphospecies) were characterized micropterous. Macropterous wasps were abundant and morphospecies rich across both sweep and pitfall collection methods, but micropterous wasps were almost exclusively captured in pitfall traps (Table 3).

Table 3: Species or morphospecies richness and abundance of ants, macropterous wasps, and micropterous wasps collected from sweep netting and pitfall trapping. Sample-based abundance values are noted parenthetically for ants.

Predatory hymenopteran assemblage metric	Pitfall collections	Sweep collections
Ant richness	7	6
Ant abundance	2555 (939)	104 (104)
Macropterous wasp richness	146	199
Macropterous wasp abundance	496	357
Micropterous wasp richness	37	2
Micropterous wasp abundance	237	2

3.2 Rarefaction and species accumulation curves.

The rarefied species accumulation curve reached an asymptote for ant species, indicating that the level of sampling employed in this study characterized the whole of ant species richness in the study area. However, the rarefied species accumulation curves did not reach an asymptote for macropterous or micropterous wasp species, suggesting that there are more species of macropterous and micropterous wasps present within the study area than were sampled in this study.

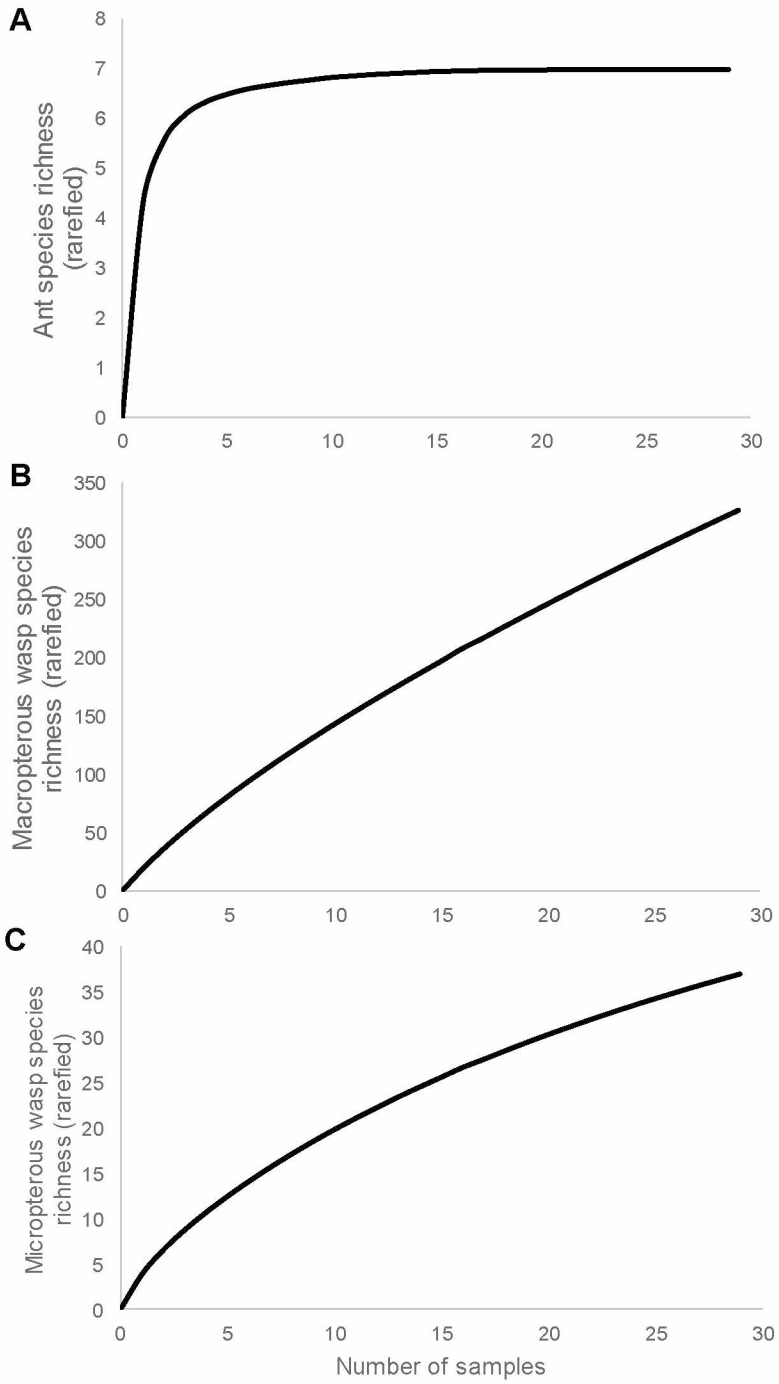

Figure 2: Species accumulation curves for sample-based rarefaction of ants (A), macropterous wasps (B), and micropterous wasps (C).

3.3 Addressing spatial autocorrelation.

When the averages of key environmental characteristics of the study sites were compared to the permuted, random subsamples drawn from the full set of LTER network sites

within an age class, in no case was the mean value for the study sites significantly more extreme than the larger set of LTER RSN sites (Table 4). There was therefore no evidence that the study sites were biased with respect to slope, aspect, soil moisture potential, or organic matter depth relative to sites in the full LTER network of similar age, despite the fact that the full LTER network covers approximately 3x more area.

Table 4: Table comparing underlying environmental variables at sampled young (n = 13) and intermediate-aged (n = 12) sites versus averages of simulated site subsets of the entire BNZ LTER RSN. Simulations were based on 1000 permutations of randomly drawn site subsets equal in sample size to study site sample size. Two-tailed *p*-values were estimated as number of simulations in which the mean was at least as extreme as the study site sample mean. Bold denotes statistical significance ($\alpha = 0.05$).

	Site age class					
	Young			**Intermediate**		
Environmental variables	sampled mean	simulated mean	*p*	sampled mean	simulated mean	*p*
Slope (deg)	4.1	5.3	0.232	4.1	6.7	0.109
Aspect (deg)	187	196	0.745	163	169	0.810
Soil moisture potential	3.5	3.2	0.329	3.3	3.3	1.000
Soil organic layer depth (cm)	3.3	6.1	0.135	13.0	11.7	0.578

The environmental variables measured at the sites did not follow patterns predicted from global climatic gradients (Table 5). Latitude was only weakly correlated with soil moisture and minimum soil temperature, and moderately positively, rather than negatively, correlated with mean soil temperature. Elevation was not correlated with soil moisture or mean temperature, and only weakly correlated to minimum soil temperature. Within the scale of this study, local processes were more important than latitude and elevation in determining site abiotic properties.

Table 5: Pearson's correlations (*r*) of spatial variables (latitude and elevation) and underlying environmental variables of sites. Bold denotes "moderate" correlation ($r \geq 0.30$).

Environmental variables	Latitude	Elevation
Slope	0.07	-0.01
Aspect	0.03	-0.21
Soil moisture potential	-0.22	-0.06
Soil temperature (mean)	**0.32**	0.09
Soil temperature (minimum)	0.16	0.21

There was little evidence that latitude or elevation influenced hymenopteran assemblages. Contrary to the generally accepted biogeographical pattern, ant richness, abundance, and biomass were strongly positively correlated with latitude (Table 6). Ant richness, abundance, and biomass were moderately negatively associated with elevation. The relationship between ants and elevation should be interpreted with caution, however, because there was a moderate negative association between latitude and elevation (-0.40). Macropterous wasp richness was weakly negatively correlated with latitude. Micropterous wasp richness was weakly positively correlated with elevation. Macropterous and micropterous wasp abundances were not correlated with either latitude or elevation (Table 6). Overall, the relationships between wasps and spatial traits were weak and inconsistent, suggesting elevation and latitude imposed relatively little influence over hymenopteran assemblages.

Table 6: Pearson's correlations (*r*) of predatory hymenopteran assemblage metrics and spatial variables of sites. Bold denotes "moderate" correlation ($r \geq 0.30$), bold and underline denotes "strong" correlation ($r \geq 0.50$).

Predatory hymenopteran assemblage metrics	Spatial variables	
	Latitude	Elevation
Ant richness	**0.58**	**-0.39**
Ant abundance	**0.56**	**-0.35**
Ant biomass	**0.52**	**-0.36**
Macropterous wasp richness	-0.12	-0.03
Macropterous wasp abundance	0.05	-0.01
Micropterous wasp richness	0.02	0.19
Micropterous wasp abundance	0.08	0.04

3.4 Predatory hymenopterans and forest composition.

To characterize how understory and overstory structure and tree species were associated with predatory hymenopteran richness, abundance, and in the case of ants, biomass, a multimodal inference approach was used to describe the relationship between predatory hymenopteran assemblage metrics and tree characteristics. The adjusted R^2 (fit) and Cohen's f^2 (effect size), of the full models show that this modeling procedure was particularly effective at describing the relationships between forest characteristics and ant, macropterous, and micropterous wasp abundances, ant species richness, and macropterous wasp morphospecies richness. The effect size was smaller for the model of micropterous wasp morphospecies richness, indicating that our ability to infer the drivers of micropterous wasp richness was more limited, and that this model was likely missing other variables of importance (Table 7). (For a table of relative importance values for each model, see Appendix A, Table A-2).

Table 7: Characteristics of full models including all parameters for each predatory hymenopteran response variable. All models have 6,22 degrees of freedom. The Cohen's f^2 metric of effect size is based on the adjusted R^2 value.

Predatory hymenopteran assemblage models	R^2	adj.R^2	F	*p*	Cohen's f^2	effect size
Ant richness	0.50	0.36	3.66	0.011	0.57	large
Ant abundance	0.71	0.63	9.09	0.000	1.73	large
Ant biomass	0.43	0.27	2.74	0.038	0.37	large
Macropterous wasp richness	0.43	0.27	2.74	0.039	0.37	large
Macropterous wasp abundance	0.43	0.28	2.78	0.037	0.38	large
Micropterous wasp richness	0.30	0.11	1.57	0.204	0.12	small-medium
Micropterous wasp abundance	0.59	0.47	5.17	0.002	0.89	large

Both ant species richness and abundance were negatively related to aspen, birch, and black spruce overstory (Table 8A). Ant species richness was also positively, but only weakly, related to aspen understory (Table 8A). Ant biomass was negatively related to birch overstory, but not associated with aspen or black spruce overstory (Table 8A). In all cases, ant metrics were most strongly negatively associated with birch overstory. The magnitude of negative relationships with aspen overstory was weakest, relative to other tree species.

Macropterous wasp richness and abundance were positively associated with aspen understory and birch overstory (Table 8B). Based on the magnitude of the coefficients, aspen understory was more strongly associated with increases in macropterous wasp abundance and richness than birch overstory. Macropterous wasp abundance was also negatively associated with birch understory.

Like macropterous wasps, micropterous wasp abundance was positively associated with aspen understory and birch overstory, though again the positive relationship with aspen understory was stronger than the relationship with birch overstory (Table 8C). Micropterous wasp abundance was also negatively associated with black spruce understory, black spruce overstory, and birch understory (Table 8C). Micropterous wasp richness was negatively

associated with black spruce overstory (Table 8C), but as mentioned previously the modeling procedure overall was weak at explaining relationships of micropterous wasp richness.

Table 8: Table of conditional model-averaged parameter coefficients with adjusted standard errors and 85% confidence intervals for all ant (A), macropterous wasp (B), and micropterous wasp (C) response variables. Parameters with coefficient 85% confidence intervals that do not overlap zero are denoted in bold. For ease of use, bolded positive relationships are denoted in red and bolded negative relationships are denoted in blue.

A) Ants	Ant richness			Ant abundance			Ant biomass		
Model parameter	β	adj. SE	85% CI	β	adj.SE	85% CI	β	adj.SE	85% CI
intercept	***1.53***	***0.15***	***1.31 , 1.75***	***3.62***	***0.23***	***3.29 , 3.95***	***4.04***	***0.30***	***3.62 , 4.47***
Aspen understory	0.14	0.10	0.00 , 0.28	0.20	0.15	-0.01 , 0.42	0.18	0.23	-0.15 , 0.51
Aspen overstory	**-0.02**	**0.01**	**-0.04 , -0.01**	**-0.04**	**0.02**	**-0.07 , -0.01**	-0.04	0.03	-0.08 , 0.01
Birch understory	0.07	0.12	-0.11 , 0.25	0.03	0.18	-0.23 , 0.29	0.07	0.28	-0.32 , 0.47
Birch overstory	**-0.08**	**0.04**	**-0.14 , -0.03**	**-0.22**	**0.06**	**-0.31 , -0.13**	**-0.22**	**0.08**	**-0.34 , -0.11**
Black spruce understory	0.00	0.05	-0.06 , 0.07	0.06	0.07	-0.04 , 0.16	0.05	0.10	-0.10 , 0.19
Black spruce overstory	**-0.05**	**0.03**	**-0.08 , -0.01**	**-0.07**	**0.04**	**-0.12 , -0.12**	-0.08	0.06	-0.16 , 0.01

B) Macropterous wasps	Macropterous richness			Macropterous abundance		
Model parameter	β	adj.SE	85% CI	β	adj.SE	85% CI
intercept	***15.13***	***2.03***	***12.26 , 18.00***	***4.66***	***0.39***	***4.09 , 5.22***
Aspen understory	**4.12**	**1.43**	**2.10 , 6.15**	**0.71**	**0.28**	**0.31 , 1.11**
Aspen overstory	0.13	0.20	-0.15 , 0.40	0.04	0.04	-0.01 , 0.09
Birch understory	-1.04	1.92	-3.76 , 1.67	**-0.47**	**0.33**	**-0.94 , -0.01**
Birch overstory	**1.38**	**0.48**	**0.70 , 2.07**	**0.20**	**0.09**	**0.07 , 0.32**
Black spruce understory	-0.19	0.66	-1.12 , 0.74	-0.09	0.12	-0.25 , 0.08
Black spruce overstory	0.03	0.37	-0.50 , 0.55	-0.02	0.07	-0.12 , 0.08

C) Micropterous wasps	Micropterous richness			Micropterous abundance		
Model parameter	β	adj.SE	85% CI	β	adj.SE	85% CI
intercept	***4.06***	***0.58***	***3.23 , 4.88***	***2.48***	***0.36***	**1.96 , 2.99**
Aspen understory	0.47	0.42	-0.12 , 1.07	**0.66**	**0.23**	**0.34 , 0.99**
Aspen overstory	0.00	0.06	-0.08 , 0.08	-0.02	0.03	-0.06 , 0.03
Birch understory	-0.36	0.51	-1.08 , 0.36	**-0.74**	**0.26**	**-1.11 , -0.38**
Birch overstory	0.18	0.15	-0.04 , 0.39	**0.23**	**0.08**	**0.12 , 0.33**
Black spruce understory	-0.22	0.17	-0.46 , 0.03	**-0.17**	**0.09**	**-0.29 , -0.04**
Black spruce overstory	**-0.15**	**0.09**	**-0.29 , -0.02**	**-0.08**	**0.05**	**-0.15 , -0.01**

3.5 Predatory hymenopterans and successional age.

Significantly more ant species were collected from early-successional sites than from mid-late successional sites (Table 9). On average, there were two more ant species collected from early-successional sites than mid-late successional sites (early-successional: mean = 5

species, SE = 0; mid-late successional: mean = 3 species, SE = 0) (Figure 3A). Additionally, significantly more ant occurrences were collected from early successional sites than from mid-late successional sites (Table 9). On average, there were 140% more ant occurrences in early-successional sites than in mid-late successional sites (early-successional: mean = 53 ant occurrences, SE = 9; mid-late successional: mean = 22 ant occurrences, SE = 5) (Figure 3B). Ant biomass was, on average, 200% higher in early-successional sites (mean = 0.09 mg/m^2 per sampling period, SE = 0.022) than in mid-late successional sites (mean = 0.03 mg/m^2, SE = 0.008), a statistically significant difference (Table 9).

In contrast, neither macropterous nor micropterous wasp assemblages varied by successional age (Figure 3C-F). There were no significant differences in macropterous or micropterous wasp richness or abundance between early and mid-late successional sites (Table 9).

Table 9: Two-sample *t*-test results comparing predatory hymenopteran assemblage metrics by successional age (early/mid-late) categories (df = 27). Bold *p* value denotes statistical significance (α = 0.05).

Predatory hymenopteran assemblage metrics	***t***	***p***
Ant richness	-2.61	**0.015**
Ant abundance	-2.82	**0.009**
Ant biomass	-2.26	**0.032**
Macropterous wasp richness	-0.12	0.902
Macropterous wasp abundance	-0.39	0.703
Micropterous wasp richness	-1.41	0.169
Micropterous wasp abundance	-1.19	0.245

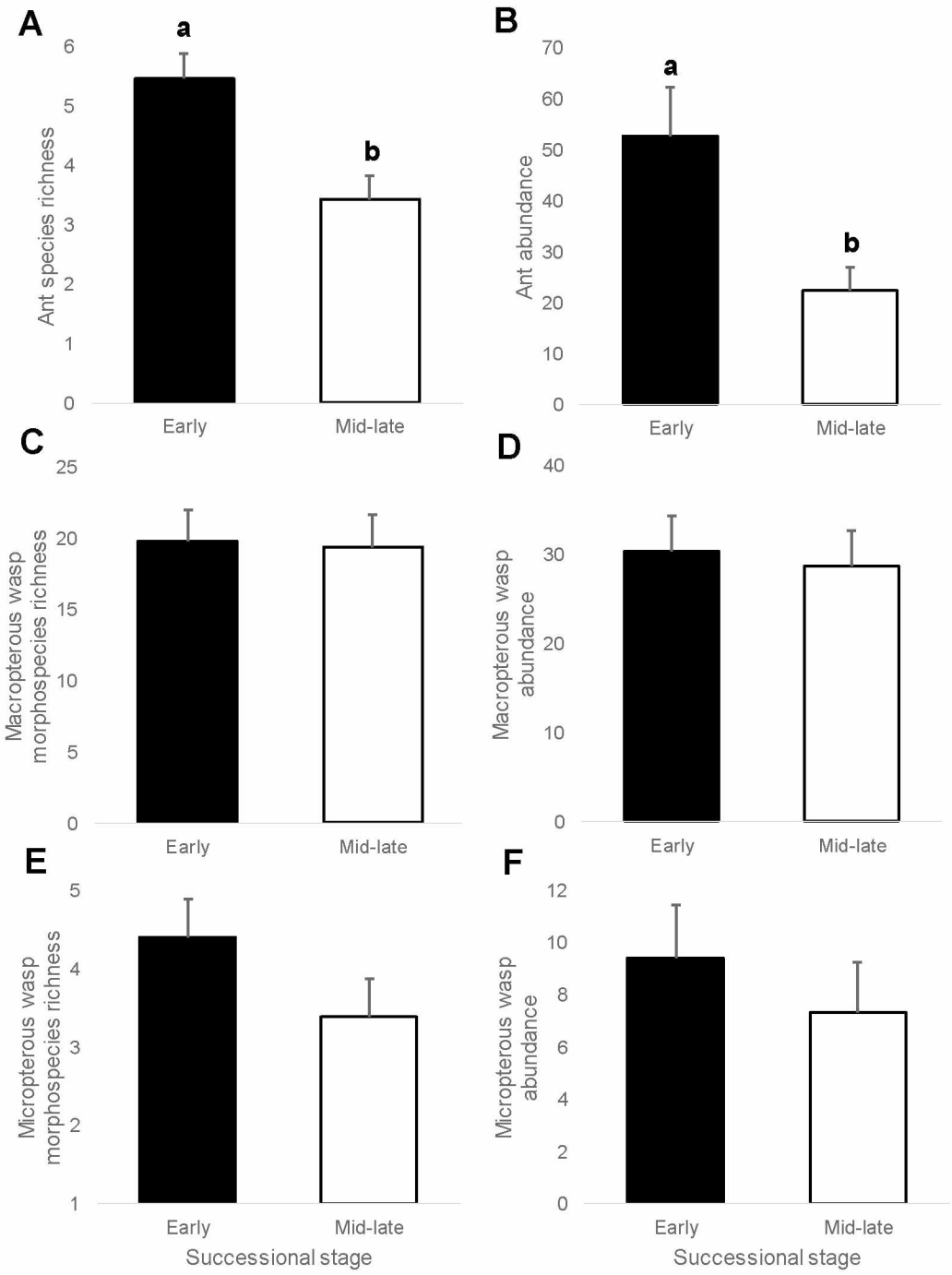

Figure 3: Mean richness and abundance of ants, macropterous wasps, and micropterous wasps by successional age (early/mid-late) categories. Error bars represent standard errors. Lower case letters above bars indicate statistically significant differences between the means (two-sample *t*-test).

3.6 Predatory hymenopteran assemblage composition.

Ant assemblage composition differed significantly among both forest composition and successional age categories (MRPP: T = -4.58, A = 0.11, p = 0.001). The pairwise comparisons among forest categories indicated that the assemblage composition of ants differed significantly between early-successional aspen sites and mid-late successional aspen sites, with a moderate effect size (Table 10A). After serial Bonferroni adjustment, there was a marginally significant difference in ant assemblage composition between mid-late successional aspen and non-aspen sites, suggesting that forest composition may have some impact on ant assemblage composition (Table 10A). The indicator species analysis of the associations of each ant species with forest categories showed that four species of ants, *Leptothorax muscorum*, *Formica aserva*, *F. subaenescens*, and *F. podzolica*, were strongly associated with early-successional aspen stands (Table 11). The results of the indicator species analysis were largely consistent with the frequency with which ants were collected from sites of each of the four forest categories (Figure 4).

Table 10: Pairwise comparisons from MRPP of ants (A), macropterous wasps (B), and micropterous wasps (C) by forest composition and successional age categories. The test statistic, T, represents the separation among groups, where more negative values indicate stronger separation. A is the chance-corrected within-group agreement, which shows how similar the values within categories are to one another, where more positive values indicate more homogeneity than would be expected by chance. A also serves as a measure of effect size. All p-values were assessed for significance using a serial Bonferroni correction (Holm's method), and those that are statistically significant are represented in bold (family-wise $\alpha = 0.05$).

(A) Ants	*T*	*A*	*p*
Early aspen vs early non-aspen	-1.33	0.03	0.102
Mid-late aspen vs mid-late non-aspen	-2.15	0.06	0.037
Early aspen vs mid-late aspen	-4.17	0.21	**0.005**
Early non-aspen vs mid-late non-aspen	-0.94	0.02	0.159
(B) Macropterous wasps	*T*	*A*	*p*
Early aspen vs early non-aspen	-2.25	0.02	**0.024**
Mid-late aspen vs mid-late non-aspen	-5.72	0.04	**0.000**
Early aspen vs mid-late aspen	-5.69	0.10	**0.001**
Early non-aspen vs mid-late non-aspen	0.20	0.00	0.546
(C) Micropterous wasps	*T*	*A*	*p*
Early aspen vs early non-aspen	-0.31	0.01	0.327
Mid-late aspen vs mid-late non-aspen	-0.93	0.01	0.165
Early aspen vs mid-late aspen	0.05	0.00	0.484
Early non-aspen vs mid-late non-aspen	-2.27	0.03	0.030

Table 11: Observed versus simulated indicator values (IV) for ant species. Displayed forest category represents the group that ant species is most indicative of (degree to which they are always and only found in that habitat type). Bold *p* denotes statistical significance (α = 0.05).

			Randomized IV		
Ant species	**Forest category**	**Observ. IV**	**Mean**	**St. dev**	***p***
Myrmica alaskensis	Early non-aspen	34.0	34.1	5.2	0.447
Leptothorax muscorum	Early aspen	72.9	36.2	10.8	**0.002**
Camponotus herculeanus	Early aspen	43.3	34.4	5.9	0.082
Formica aserva	Early aspen	45.3	25.9	9.0	**0.037**
Formica neorufibarbis	Early non-aspen	35.2	28.6	8.7	0.201
Formica subaenescens	Early aspen	46.8	31.2	7.0	**0.033**
Formica podzolica	Early aspen	47.8	20.2	10.4	**0.018**

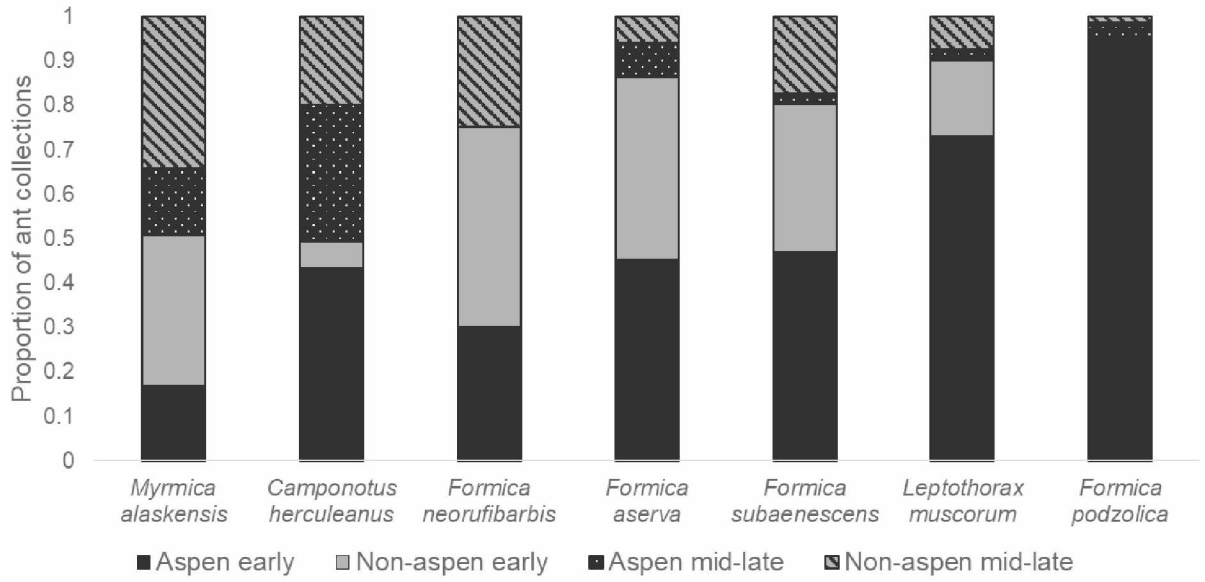

Figure 4: Proportion of ant species collected by forest composition (aspen/non-aspen) and successional age (early/mid-late) categories. Proportions were standardized by the number of sites that constituted each forest category.

Macropterous wasp assemblage composition differed significantly among the four forest categories (MRPP: $T = -7.04$, $A = 0.05$, $p < 0.0001$). The pairwise comparisons among forest categories showed that the composition of macropterous wasps differed significantly between

aspen and non-aspen sites in both early and mid-late successional groups, however the effect size (*A*) was relatively weak for these groups, indicating that these differences may not be of ecological significance (Table 10B). Assemblage composition also differed significantly between early-successional aspen and mid-late successional aspen sites, suggesting that wasp species composition changes as aspen stands age.

The MRPP results indicated that forest characteristics may be related to micropterous wasp assemblage composition (MRPP: $T = -1.61$, $A = 0.02$, $p = 0.066$); however, the pairwise comparisons showed no significant differences among forest categories (Table 10C).

3.7 Predatory hymenopterans and their relationships with environmental variables.

In general, ant species richness and biomass were poorly related to soil microclimate. Ant species richness and biomass were weakly positively correlated with mean soil temperature, but no correlation was detected between ant species richness or biomass and soil moisture potential or minimum soil temperature (Table 12). Ant abundance was somewhat more correlated with soil microclimate (Table 12). Ant abundance had a weak, positive relationship to soil moisture and a moderate positive relationship to mean soil temperature, but was not correlated with minimum soil temperature. Slope was not important in describing ant assemblages. Ant species richness, abundance, and biomass had strong negative relationships with canopy cover (Table 12).

Macropterous wasp abundance was more strongly related to environmental variables than macropterous wasp richness. Macropterous wasp abundance had moderate positive relationships with mean and minimum soil temperatures, whereas macropterous wasp morphospecies richness was only weakly related to soil temperatures (Table 12). Both macropterous wasp richness and abundance had moderate negative relationships with soil moisture potential. Macropterous wasp richness and abundance were weakly negatively related

to slope (Table 12). Both macropterous wasp richness and abundance were weakly positively related to percent canopy cover.

Micropterous wasp richness and abundance were unrelated to soil moisture, however, were somewhat positively correlated with both mean and minimum soil temperatures (Table 12). Both micropterous wasp richness and abundance were negatively related to slope (Table 12). Micropterous wasps were not correlated to percent canopy cover.

Table 12: Pearson's correlations (*r*) of predatory hymenopteran assemblage metrics and environmental variables of sites. Bold denotes "moderate" correlation ($r \geq 0.30$), bold and underline denotes "strong" correlation ($r \geq 0.50$).

	Environmental variables				
Predatory hymenopteran assemblage metrics	Soil moisture	Soil temp. (mean)	Soil temp. (min.)	Slope	Canopy cover
Ant richness	-0.04	0.27	0.06	0.11	**-0.62**
Ant abundance	0.13	**0.30**	-0.04	0.01	**-0.75**
Ant biomass	0.01	0.27	-0.01	0.03	**-0.62**
Macropterous wasp richness	**-0.34**	0.22	0.26	-0.12	0.26
Macropterous wasp abundance	**-0.42**	**0.36**	**0.46**	-0.18	0.22
Micropterous wasp richness	0.02	**0.33**	**0.32**	**-0.50**	-0.10
Micropterous wasp abundance	-0.03	0.18	0.28	**-0.44**	0.02

As expected, aspen was associated with warm, well-drained soil conditions. Soil moisture was strongly negatively related to the percent of aspen at a site (Pearson's $r = -0.55$) (Figure 5A). Mean and minimum soil temperatures were strongly positively related to percent aspen (Pearson's $r = 0.66$, $r = 0.79$, respectively) (Figure 5B).

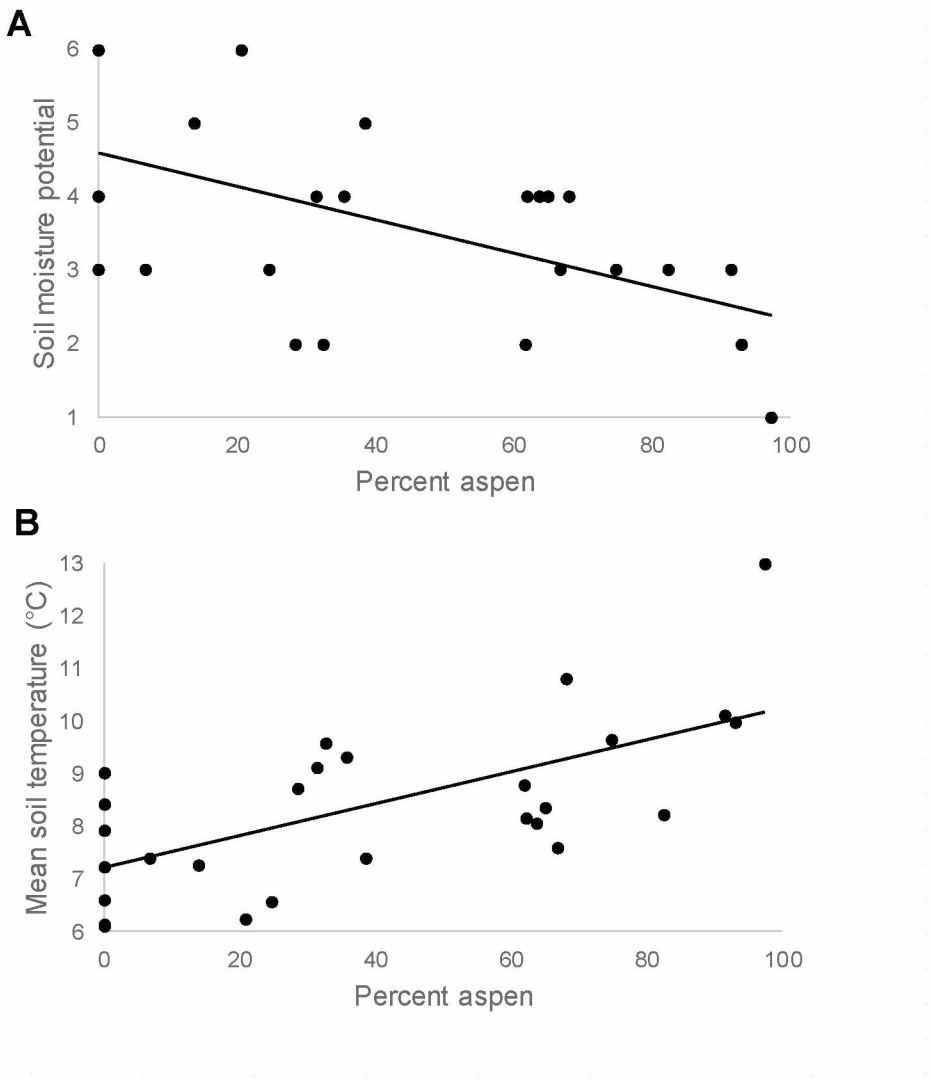

Figure 5: Relationships between the relative basal area of aspen (%) at a site and the site's soil moisture potential (A) and mean soil temperature (B).

4 Discussion

4.1 Predatory hymenopterans and their relationship to forest composition.

The results of this study suggest that ant assemblages are not strongly influenced by forest composition. Overall, ant richness, abundance, and biomass were not strongly associated

with aspen over other tree species. This does not support the hypothesis that aspen, through the provisioning of extrafloral nectar and increased palatability, supports more abundant and species-rich ant assemblages; a surprising result given that ants are the predominant visitors of extrafloral nectaries (Heil 2015). However, in this study we characterized the ant assemblage as a whole, not just those ant species that commonly use foliar resources. From the modeling procedure, we found that the magnitude of the aspen understory coefficient was relatively large for all ant assemblage metrics, but the variability around that coefficient was also high. Ants are opportunistic foragers, and this result suggests that some species of ants may be influenced by forest composition in some successional contexts. The indicator-species analysis shows that four of the seven species of ants were associated specifically with early-successional aspen sites. This suggests that for some ant species in interior Alaska, early-successional aspen stands may provide critical resources such as extrafloral nectar or prey availability.

In contrast to ants, macropterous and micropterous wasps showed clear associations with forest composition. It is likely that some combination of extrafloral nectar and plant palatability drive the relationships between forest composition and wasp assemblages. An association between macropterous wasp abundance and richness and the basal area of aspen seedlings and saplings is consistent with the idea that extrafloral nectar may influence these assemblages in the boreal forest. Extrafloral nectary expression is more frequent on smaller aspen than on larger-sized aspen (Doak et al. 2007), which could explain why macropterous wasps had stronger relationships with aspen seedlings and saplings than with mature aspen trees. While overstory trees produce more leaves than small trees, the effort required by wasps to locate nectar may be greater in the mature aspen trees of mid-late successional forests than in the smaller trees of early-successional forests. In this way, extrafloral nectar may therefore be more efficiently located in early-successional forests, which may explain why macropterous wasps were most abundant and morphospecies rich in early-successional aspen stands. However, because micropterous wasps, by virtue of tiny size and limited mobility, are unlikely to

access foliar resources such as extrafloral nectar, a more parsimonious explanation is that both micropterous and macropterous wasp abundances were positively associated with aspen seedlings and saplings for reasons other than extrafloral nectar. While predatory and parasitoid wasps may be important consumers of extrafloral nectar, studies exploring their assemblage composition in the context of extrafloral nectar, to our knowledge, do not exist (Heil 2015).

The positive relationships that macropterous wasp assemblages had with aspen seedlings and saplings and mature birch trees are also consistent with the idea that plant palatability, acting through its effects on the prey base, may influence these assemblages. The evidence for prey availability as an influential factor stems from the observations that both macropterous and micropterous wasp abundances were negatively associated with birch seedlings and saplings, but positively associated with mature birch trees. Younger hardwood trees tend to invest more energy into defense than more mature trees (Bryant et al. 1983), which may support more palatable herbivores as prey for predators (Price et al. 1980). Additionally, overstory trees offer more structural niches than understory vegetation, and typically are associated with increased herbivore diversity (Lawton 1983). Because conifer species tend to invest more energy in defense than hardwood species, the strong negative relationships that micropterous wasp richness and abundance have with black spruce were also consistent with the idea that prey may structure these wasp assemblages. However, distributional patterns of macropterous wasps differed from those of micropterous wasps in this regard and did not have strong negative relationships with black spruce, which suggests that macropterous and micropterous wasps may respond to different factors. Additionally, the relationships between wasps and aspen were inconsistent with what would be expected if prey availability alone were driving these assemblages. Macropterous wasp abundance and richness, and micropterous wasp abundance, were positively influenced by aspen seedlings and saplings, but not by mature aspen. This contradicts the palatability hypothesis because smaller aspen seedlings and saplings produce more phenolic glycosides and should be less

palatable than larger, mature aspen (Donaldson et al. 2006, Young et al. 2010). While the relationships between wasp assemblages and forest composition were not wholly consistent with extrafloral nectar or plant palatability alone, some combination of these potential influences may explain the observed patterns in predatory hymenopteran assemblages.

It is also possible that microclimatic factors associated with aspen stands may contribute to the association between predatory hymenopteran assemblages and aspen. The relative abundance of aspen was negatively associated with soil moisture and positively associated with soil temperature, which may explain some of the reasons why predatory hymenopterans were associated with aspen. While macropterous wasps were the only predatory hymenopterans with moderate negative relationships to soil moisture, all predatory hymenopteran groups were positively associated with soil temperature. The correlations between soil temperature and the abundance and richness of ants, macropterous wasps, and micropterous wasps were consistently positive but ranged from weak to moderate, suggesting temperature is important for predatory hymenopterans, but is likely not solely responsible for the patterns seen in these assemblages. Unexpectedly, macropterous wasps were more strongly negatively associated with soil moisture than ants or micropterous wasps, and were similarly positively associated with soil temperature. This contradicts the prediction that ants and micropterous wasps would be more directly dependent upon soil properties than macropterous wasps. Interestingly, micropterous wasp morphospecies richness and abundance were, respectively, strongly and moderately negatively related to slope across sites (Table 12). Sites with steeper slopes may accumulate a shallower layer of leaf litter necessary to sustain micropterous wasp assemblages.

4.2 Predatory hymenopteran assemblages and post-fire successional time.

This study provides evidence that changes occur in ant assemblages during post-fire succession. Ant assemblages were significantly more species-rich and abundant in early-

successional forests compared to mid-late successional forests, and ant assemblage composition differed significantly between early- and mid-late-successional aspen stands. Previous studies in eastern Nearctic boreal black-spruce forests (Quebec, Canada) found that, in general, abundance of ant nests increased throughout the first 30 years after fire, but ant nest abundance was strongly reduced by year 62 post-fire (Boucher et al. 2015). This general pattern holds true for our study as well; ant occurrences were most frequent in early-successional sites, burned in 2004. However, the patterns of species composition have not been consistent across studies. In the Quebec boreal forest, *C. herculeanus* and *F. neorufibarbis* were predominantly found in 60-year old burn sites, suggesting these species thrive late in post-fire succession (Boucher et al. 2015), whereas a study of post-logging succession in sub-boreal lodgpole pine forests (British Columbia, Canada) found that both *C. herculeanus* and *F. neorufibarbis* were found in regenerating forests up to 25 years post-harvest (early succession), but were not present in unharvested sites (late succession) (Higgins and Lindgren 2015). The assemblage composition results of our study were consistent with aspects of both previous studies, in that both *C. herculeanus* and *F. neorufibarbis* were represented in both early- and mid-late-successional forests. These species apparently arrive early in post-fire succession, and unlike many other Alaskan formicine species, they also persist into later successional stages (Figure 4).

The facultative wood-nesting behavior of some ant species may facilitate their persistence into the later successional stages. Wood can provide a warmer nesting substrate than soil (Higgins and Lindgren 2012). In particular, *C. herculeanus*, *F. neorufibarbis*, and *M. alaskensis* have been frequently observed as wood nesters (Francoeur 1997), which is consistent with the frequencies of which these species have been observed in our study in early-successional forests relative to other, predominantly soil-nesting, species (Figure 4). Our results are similar to those from sub-boreal forests of British Columbia, Canada, which found that *M. alaskensis* persisted into later successional stages and was particularly cold-tolerant

(Higgins 2010). Results from sub-boreal studies of *F. aserva* and *L. muscorum* found that these species are sensitive to advances in succession, because the canopy shading in older successional forests prevents nest heat gain from insolation (Higgins 2010, Higgins and Lindgren 2012). Consistent with these results, we collected *F. aserva* and *L. muscorum* predominantly from early-successional aspen stands (Figure 4), where the warmest mean soil temperatures were observed (early-successional aspen: 10.5 ± 0.98 °C, mid-late successional aspen: 8.7 ± 0.33 °C, early-successional non-aspen: 7.9 ± 0.40 °C, mid-late successional non-aspen: 7.5 ± 0.41 °C).

In contrast to ants, we found little evidence that macropterous wasp assemblages, and no evidence that micropterous wasp assemblages, were influenced by successional age. The abundance and morphospecies richness of both macropterous and micropterous wasps were similar between early-successional and mid-late successional forests. However, based on the MRPP analysis, the composition of macropterous wasp assemblages did differ between early- and mid-late-successional aspen stands. In contrast, there were no differences in composition of micropterous wasp assemblages between early- and mid-late-successional stands. The MRPP analysis was likely a conservative comparison of wasp assemblage composition among habitats in this study, because wasp assemblages were composed of many rare individuals, making the compositional similarities inherently difficult to characterize. MRPP relies not only on the differences in composition between two forest categories, but also the agreement, or similarities, of sites within a forest category, and therefore it may have been difficult for this analysis to detect patterns of wasp assemblage composition. Future research should increase sampling intensity of these assemblages, to better match the magnitude of species diversity of boreal wasp assemblages.

4.3 Spatial considerations of forest composition and successional age.

It is unlikely that patterns of hymenopteran abundance and richness reported in this study are due to inadequacies in spatial dispersion among sites of different compositions or successional ages. The positive relationship between ant assemblage metrics and latitude ran contrary to the classic biogeographic pattern and thus ant species richness, abundance, and biomass were clearly better explained by successional age than latitude. The basal areas of aspen, black spruce, and birch in this study were unrelated to latitudinal and elevational gradients. Furthermore, the associations between predatory hymenopterans and forest compositions cannot be explained by our general understanding of how increases in elevation reduce hymenopteran abundance and species richness.

It is worth noting that the differences in latitude and elevation in this study were relatively small compared to those of studies intended to investigate geographical trends. The latitudinal gradient in this study spanned only 2.4°, whereas gradients in other studies regarding hymenopteran patterns in space spanned at least 20° in latitude (Janzen and Pond 1975, Cushman et al. 1993). The elevational difference from lowest to highest elevation sites in this study spanned only 641 m, whereas other studies have spanned 2090 m (Janzen and Pond 1975). Furthermore, the difference in average elevation between young and intermediate-aged sites was less than 100 m (young: 316 m, intermediate: 410 m).

4.4 Implications of a changing boreal forest on predatory hymenopteran assemblages.

As climate-driven changes in the boreal fire regime increase in magnitude, the resulting changes in boreal vegetation communities (Hollingsworth et al. 2013) are likely to influence predatory hymenopteran assemblages. Because aspen persistence is favored by frequent and severe fires, aspen will likely become more widely distributed on the landscape (Johnstone and

Kasischke 2005, Johnstone et al. 2010b). Based on our results, increased aspen prevalence on the landscape would increase the species richness of macropterous wasps, and to a lesser extent ants, as well as the abundance of macropterous and micropterous wasps. Additionally, an increase in forest fire frequency and extent will increase the proportion of forests in younger successional stages. Our results indicate that this will increase the species richness and abundance of ants on the landscape. Conversely, many of the micropterous wasps are thought to dwell within leaf litter, and frequent, severe burns may reduce the available habitat for these species. Furthermore, because they lack wings, many of these species may be dispersal-limited. If fires increase in frequency to the point that these litter-dwelling wasps have little time to establish, or fires expand in extent to the point of severely hindering their dispersal capabilities, then species diversity may decline throughout interior Alaska.

Northern high-latitude biomes, including the boreal forest, are warming at twice the average global rate (IPCC 2013). Climate change has altered forest and vegetation composition (Hollingsworth et al. 2013) in ways that will cascade to forest-associated animal communities. This study increases our baseline understanding of the assemblage composition and distribution of predatory hymenopterans, including litter and soil-dwelling Hymenoptera. Litter and soil-dwelling Hymenoptera are exceptionally diverse, and have been estimated to represent up to 30% of the soil-associated fauna in temperate beech forests (Ulrich 2004). Despite their numbers, micropterous Hymenoptera have been especially overlooked, not just in the boreal forest, but globally (Ulrich 2004, Silva and Feitosa 2017). To our knowledge, this study is the first to characterize the composition of micropterous wasp assemblages and their relationships with forest characteristics in the boreal forest. The wasp individuals captured in this study represented a wide diversity of taxa, and because the species accumulation curves were unsaturated and many of the morphospecies captures were singletons, the diversity of wasps detected in this study represents only a fraction of the total diversity in the boreal forest. Sampling methods specifically designed to target these organisms, such as via use of Winkler

or Burlese funnels, may yield a more thorough representation of the soil and litter associated hymenopterans of boreal Alaska (Silva and Feitosa 2017).

5 Conclusions

Predatory hymenopteran assemblages vary considerably among forests composed of different tree species and stand structures. Macropterous wasps, and to a lesser extent ants, were most species-rich in forest stands composed of aspen seedlings and saplings relative to birch and black spruce. Both macropterous and micropterous wasps were most abundant in stands composed of aspen seedlings and saplings. While it was not possible to disentangle the mechanisms that drive the distribution of predatory hymenopteran assemblages using observational data, the patterns are consistent with the influence of extrafloral nectar provisioning, foliage palatability, and microclimatic preferences shared by both aspen and predatory hymenopterans. Predatory hymenopteran assemblage patterns were not wholly consistent with any one of these mechanisms alone, but a combination of these factors could explain their distributions.

There was little evidence that macropterous or micropterous wasps were influenced by post-fire succession, however, the strong negative associations between ants and mid-late successional forests suggest that ants decline in abundance and species richness as post-fire succession proceeds. These changes in ant assemblages are consistent with differences in soil microclimate and with other studies that have addressed the thermophilic nature of ants.

Future, climate-induced changes in the boreal forest fire regime are likely to alter the distribution and composition of predatory hymenopteran assemblages. Changes to the fire regime that result in an increase in the prevalence of aspen on the landscape could increase the abundance of macropterous wasps and ants, and the species richness of macropterous and micropterous wasps. Increases in fire frequency and severity, resulting in an increase in the

proportion of forest in younger successional stages, will likely increase suitable habitat for ants, and increase the abundance, species richness, and biomass of ants across the landscape.

6 References

AntWeb. 2014. https://www.antweb.org. California Academy of Sciences.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management **74**:1175-1178.

Baraza, E., R. Zamora, and J. A. Hodar. 2006. Conditional outcomes in plant-herbivore interactions: neighbors matter. Oikos **113**:148-156.

Bennett, P. M. and K. A. Hobson. 2009. Trophic structure of a boreal forest arthropod community revealed by stable isotope (δ13C, δ15N) analyses. Entomological Science **12**:17-24.

Bentley, B. L. 1977. Extrafloral nectaries and protection by pugnacious bodyguards. Annual Review of Ecology and Systematics **8**:407-427.

Bluthgen, N. and H. Feldhaar. 2010. Food and shelter: how resources influence ant ecology. Pages 115-136 *in* L. Lach, C. Parr, and K. Abbott, editors. Ant Ecology. Oxford University Press, United States, New York.

Bonanza Creek LTER. 2014. Data catalog, http://www.lter.uaf.edu/data/data-catalog. Institute of Arctic Biology, University of Alaska Fairbanks.

Boucher, P., C. Hebert, A. Francoeur, and L. Sirois. 2015. Postfire succession of ants (Hymenoptera: Formicidae) nesting in dead wood of northern boreal forest. Environmental Entomology **44**:1316-1327.

Bryant, J. P., F. S. Chapin, and D. R. Klein. 1983. Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40**:357-368.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.

Byk, J. and K. Del-Claro. 2011. Ant-plant interaction in the neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. Population Ecology **53**:327-332.

Chen, Y.-H. and E. J. H. Robinson. 2015. The relationship between canopy cover and colony size of the wood ant *Formica lugubris* - implications for the thermal effects on a keystone ant species. Plos One **9**:e116113.

Cohen, J. 1992. A power primer. Psychological Bulletin **112**:155-159.

Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science **230**:895-899.

Cushman, J. H., J. H. Lawton, and B. F. J. Manly. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. Oecologia **95**:30-37.

Danks, H. V. and R. G. Foottit. 1989. Insects of the boreal zone of Canada. The Canadian Entomologist **121**:625-690.

Doak, P., D. Wagner, and A. Watson. 2007. Variable extrafloral nectary expression and its consequences in quaking aspen. Canadian Journal of Botany-Revue Canadienne De Botanique **85**:1-9.

Donaldson, J. R., M. T. Stevens, H. R. Barnhill, and R. L. Lindroth. 2006. Age-related shifts in leaf chemistry of clonal aspen (*Populus tremuloides*). Journal of Chemical Ecology **32**:1415-1429.

Dufrene, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. Ecological Monographs **67**:345-366.

Ellison, A. M., N. J. Gotelli, E. J. Farnsworth, and G. D. Alpert. 2012. A field guide to the ants of New England. Yale University Press, New Haven and London.

Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. The Coleopterists Bulletin **36**:74-75.

Finnegan, R. J. 1973. Diurnal foraging activity of *Formica sublucida*, *F. sanguinea subnudaris*, and *F. fossaceps* (Hymenoptera: Formicidae) in Quebec. Canadian Entomologist **105**:441-444.

Francoeur, A. 1997. Ants of the Yukon. Pages 901-910 *in* H. V. Danks and J. A. Downes, editors. Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.

Gause, G. F. 1934. The Struggle for Existence Williams and Wilkins Co., Baltimore.

Glasier, J. R. N., J. H. Acorn, S. E. Nielsen, and H. Proctor. 2013. Ants (Hymenoptera: Formicidae) of Alberta: a key to species based primarily on the worker caste. Canadian Journal of Arthropod Identification **22**:1-104.

Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters **4**:379-391.

Gotelli, N. J., A. M. Ellison, R. R. Dunn, and N. J. Sanders. 2011. Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological News **15**:13-19.

Goulet, H. and J. T. Huber. 1993. Hymenoptera of the world: an identification guide to families. Centre for Land and Biological Resources Research, Ottawa, Ontario.

Hart, S. A. and H. Y. H. Chen. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. Ecological Monographs **78**:123-140.

Heil, M. 2015. Extrafloral nectar at the plant-insect interface: a spotlight on chemical ecology, phenotypic plasticity, and food webs. Annual Review of Entomology **60**:213-232.

Herms, D. A. and W. J. Matson. 1992. The dilemma of plants: to grow or defend. The Quarterly Review of Biology **67**:283-335.

Higgins, R. J. 2010. The ant (Hymenoptera: Formicidae) communities of the central interior of British Columbia: adaptations to a temperature-constrained environment. PhD dissertation. University of Northern British Columbia, Prince George, BC, Canada.

Higgins, R. J. and B. S. Lindgren. 2006. The fine scale physical attributes of coarse woody debris and effects of surrounding stand structure on its utilization by ants (Hymenoptera: Formicidae) in British Columbia, Canada.67-74.

Higgins, R. J. and B. S. Lindgren. 2012. The effect of manipulated shading on the colony abundance of two species of ants, *Formica aserva* and *Leptothorax muscorum*, in dead wood. Entomologia Experimentalis Et Applicata **143**:292-300.

Higgins, R. J. and B. S. Lindgren. 2015. Seral changes in ant (Hymenoptera: Formicidae) assemblages in the sub-boreal forests of British Columbia. Insect Conservation and Diversity **8**:337-347.

Hollingsworth, T. N. 2015. Shrub, seedling, and sapling density at Bonanza Creek LTER research sites (1975-present). Bonanza Creek LTER - University of Alaska Fairbanks **BNZ:530**.

Hollingsworth, T. N., J. F. Johnstone, E. L. Bernhardt, and I. F. Stuart Chapin. 2013. Fire severity filters regeneration traits to shape community assembly in Alaska's boreal forest. Plos One **8**:e56033.

Hollingsworth, T. N., A. H. Lloyd, D. R. Nossov, R. W. Ruess, B. Charlton, and K. Kielland. 2010. Twenty-five years of vegetation change along a putative successional chronosequence on the Tanana River, Alaska. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **40**:15.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65-70.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2000. Conservation of insect diversity: a habitat approach. Conservation Biology **14**:1788-1797.

IPCC. 2013. Climate change 2013: the physical science basis. Working group 1 contribution to the Intergovernmental Panel on Climate Change fifth assessment report. Cambridge University Press, Cambridge.

Jamont, M., S. Crepelliere, and B. Jaloux. 2013. Effect of extrafloral nectar provisioning on the performance of the adult parasitoid *Diaeretiella rapae*. Biological Control **65**:271-277.

Janzen, D. H. and C. M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. Transactions of the Royal Entomological Society of London **127**.

Johnstone, J. F. 2005. Effects of aspen (*Populus tremuloides*) sucker removal on postfire conifer regeneration in central Alaska. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:483-486.

Johnstone, J. F., F. S. Chapin, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010a. Fire, climate change, and forest resilience in interior Alaska. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **40**:1302-1312.

Johnstone, J. F. and T. N. Hollingsworth. 2013. Environmental and stand data for sites located in the 2004 burns off the Steese, Taylor, and Dalton highways, collected in 2005-2007. Bonanza Creek LTER - University of Alaska Fairbanks **BNZ:342**:http://www.lter.uaf.edu/data/data-detail/id/342.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology **16**:1281-1295.

Johnstone, J. F., T. N. Hollingsworth, and F. S. C. III. 2008. A key for predicting postfire successional trajectories in black spruce stands of interior Alaska. USDA, Forest Service, Pacific Northwest Research Station, General Technical Report **PNW-GTR-767**:37.

Johnstone, J. F. and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere **35**:2151-2163.

Kipyatkov, V. E. and E. B. Lopatina. 2015. Comparative study of thermal reaction norms for development in ants. Entomological Science **18**:174-192.

Koptur, S. 2005. Nectar as fuel for plant protectors. Pages 75-108 *in* F. L. Wackers, P. C. J. van Rijn, and J. Bruin, editors. Plant-provided food for carnivorous insects. Cambridge University Press.

Kusnezov, N. 1957. Numbers of species of ants in faunae of different latitudes. Evolution **11**:298-299.

Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology **28**:23-39.

Lindroth, R. L. and S. B. St Clair. 2013. Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. Forest Ecology and Management **299**:14-21.

Longino, J. T., J. Coddington, and R. K. Colwell. 2002. The ant fauna of a tropical rainforest: estimating species richness three different ways. Ecology **83**:689-702.

Machac, A., M. Janda, R. R. Dunn, and N. J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. Ecography **34**:364-371.

MacKay, W. P., S. Silva, D. C. Lightfoot, M. I. Pagani, and W. G. Whitford. 1986. Effect of increased soil moisture and reduced soil temperature on a desert soil arthropod community. The American Midland Naturalist **116**:45-56.

MacKinney. 1929. Effects of forest litter on soil temperature and soil freezing in autumn and winter. Ecology **10**:312-321.

MacLean, S. F. and T. S. Jensen. 1985. Food plant selection by insect herbivores in Alaskan arctic tundra: the role of plant life form. Oikos **44**:211-221.

Majer, J. D., H. F. Recher, and A. C. Postle. 1994. Comparison of arthropod species richness in Eastern and Western Australian canopies: a contribution to the species number debate. Memoirs of the Queensland Museum **36**:121-132.

Maleque, M. A., K. Maeto, and H. T. Ishii. 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Applied Entomology and Zoology **44**:1-11.

Maleque, M. A., K. Maeto, S. I. Makino, H. Goto, H. Tanaka, M. Hasegawa, and A. Miyamoto. 2010. A chronosequence of understorey parasitic wasp assemblages in secondary broad-leaved forests in a Japanese 'satoyama' landscape. Insect Conservation and Diversity **3**:143-151.

McCune, B. and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

Mielke, P. W. 1984. Meteorological applications of permutation techniques based on distance functions. Pages 813-830 *in* P. R. Krishnaiah and P. K. Sen, editors. Handbook of Statistics. Elsevier Science Publishers.

Noyes, J. S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. Ecological Entomology **14**:197-207.

Ode, P. J. 2006. Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. Annual Review of Entomology **51**:163-185.

Palladini, J. D., M. G. Jones, N. J. Sanders, and E. S. Jules. 2007. The recovery of ant communities in regenerating temperate conifer forests. Forest Ecology and Management **242**:619-624.

Poelman, E. H., J. J. van Loon, and M. Dicke. 2008. Consequences of variation in plant defense for biodiversity at higher trophic levels. Trends Plant Sci **13**:534-541.

Politis, D. N. and J. P. Romano. 1994. Large sample confidence regions based on subsamples under minimal assumptions. The Annals of Statistics **22**:2031-2050.

Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels - influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics **11**:41-65.

Sanders, N. J., J.-P. Lessard, M. C. Fitzpatrick, and R. R. Dunn. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography **16**:640-649.

Schuur, E. A. G., A. D. McGuire, C. Schadel, G. Grosse, J. W. Harden, D. J. Hayes, G. Hugelius, C. D. Koven, P. Kuhry, D. M. Lawrence, S. M. Natali, D. Olefeldt, V. Romanovsky, K. Shaefer, M. Turetsky, C. C. Treat, and J. E. Vonk. 2015. Climate change and the permafrost carbon feedback. Nature **520**:171-179.

Shenoy, A. 2016. Role of fire severity in controlling patterns of stand dominance following wildfire in boreal forests. PhD dissertation. University of Alaska Fairbanks, Fairbanks, AK.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management **261**:381-390.

Silva, R. R., R. S. Machado Feitosa, and F. Eberhardt. 2007. Reduced ant diversity along a habitat regeneration gradient in the southern Brazilian Atlantic Forest. Forest Ecology and Management **240**:61-69.

Silva, T. S. R. and R. M. Feitosa. 2017. Hunting for wasps in-between: the use of the Winkler extractor to sample leaf litter Hymenoptera. Neotropical Entomology:1-8.

Simonson, S. E., P. A. Opler, T. J. Stohlgren, and G. W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation **10**:1369-1386.

Sobek, S., T. Tscharntke, C. Scherber, S. Schiele, and I. Steffan-Dewenter. 2009. Canopy vs. understory: does tree diversity affect bee and wasp communities and their natural enemies across forest strata? Forest Ecology and Management **258**:609-615.

Staab, M., A. Schuldt, T. Assmann, H. Bfuelheide, and A. M. Klein. 2014. Ant community structure during forest succession in a subtropical forest in South-East China. Acta Oecologica-International Journal of Ecology **61**:32-40.

Symonds, M. R. E. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology **65**:13-21.

Sznajder, B. and J. A. Harvey. 2003. Second and third trophic level effects of differences in plant species reflect dietary specialisation of herbivores and their endoparasitois. Entomologia Experimentalis Et Applicata **109**:73-82.

Ulrich, W. 2004. Soil-living parasitic Hymenoptera: comparison between a forest and an open landscape habitat. Pedobiologia **48**:59-69.

Van Cleve, K., F. S. Chapin, and R. W. Ruess. 2015. Tree inventory data taken at BCEF sites (1989-present). Bonanza Creek LTER - University of Alaska Fairbanks **BNZ:320**:http://www.lter.uaf.edu/data/data-detail/id/320.

Wäckers, F. L., P. C. J. v. Rijn, and J. Bruin. 2005. Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, UK.

Wanner, H., H. Gu, and S. Dorn. 2006. Nutritional value of floral nectar sources for flight in the parasitoid wasp, *Cotesia glomerata*. Physiological Entomology **31**:127-133.

Wendler, G. and M. Shulski. 2009. A century of climate change for Fairbanks, Alaska. Arctic **62**:295-300.

Young, B., D. Wagner, P. Doak, and T. Clausen. 2010. Within-plant distribution of phenolic glycosides and extrafloral nectaries in trembling aspen (*Populus tremuloides*; Salicaceae). American Journal of Botany **97**:601-610.

Appendix A

Table A-1: Average weight of a worker individual of each ant species in milligrams, arranged in ascending order by weight. Average worker weight is based on the dry weight of 10 worker individuals of each species.

Ant species	Mean mass (mg)	Standard error
Myrmica alaskensis	0.38	0.03
Leptothorax muscorum	0.12	0.09
Camponotus herculeanus	2.49	0.45
Formica aserva	1.40	0.11
Formica neorufibarbis	0.86	0.11
Formica subaenescens	0.54	0.08
Formica podzolica	0.63	0.07

Table A-2: Relative importance of each parameter by predatory hymenopteran assemblage metric model. Values are calculated by summing the AICc weights across all candidate models each parameter was included in. Values range between 0 and 1, with 1 indicating that parameter was included in all candidate models.

Relative importance of parameters by predatory hymenopteran assemblage model							
Model parameter	Ant richness	Ant abundance	Ant biomass	Macropterous richness	Macropterous abundance	Micropterous richness	Micropterous abundance
Aspen understory	0.42	0.38	0.24	0.98	0.94	0.34	0.97
Aspen overstory	0.59	0.61	0.32	0.21	0.34	0.17	0.17
Birch understory	0.20	0.14	0.18	0.20	0.40	0.23	0.96
Birch overstory	0.75	1.00	0.91	0.97	0.82	0.34	0.99
Black spruce understory	0.17	0.26	0.20	0.17	0.22	0.37	0.63
Black spruce overstory	0.57	0.59	0.40	0.17	0.20	0.56	0.47

Appendix B

Morphospecies character distinctions by family/superfamily

Morphospecies were named beginning with the lowest taxonomic level to which they were identified, either superfamily, family, or subfamily. Number in numbered list indicates the morphospecies identification number, which together with the lowest taxonomic identification level, corresponds to the morphospecies name. The number in parentheses indicates the number of specimens that were identified as that particular morphospecies, and the text describes the characters used to discern one morphospecies from another. For example, the first specimen under the subheading "CERAPHRONIDAE" corresponds to morphospecies *Ceraphronidae sp.01*, and the (1) indicates that there was only one specimen identified as that particular morphospecies. All specimens can be found in the University of Alaska Museum Insect Collection (accession number: UAM-2017.10-Wenninger-Ento).

CERAPHRONIDAE (CERAPHRONOIDEA):

"light/tan"

1. (1) all brown/yellow
2. (2) black head/mesosoma, brown metasoma
3. (1) yellow, last 2 antennal segments brown, flagellomeres widen apically
4. (3) large, yellow, flagellomeres brown and widen apically
5. (2) small, yellow, flagellomeres brown and widen apically
6. (8) small, yellow with black head and tip of metasoma, long/thin antennae

"dark"

7. (1) BRACHYPTEROUS, lighter legs and metasoma
8. (1) BRACHYPTEROUS, dark
9. (1) thin wing, dark, setose
10. (2) black, large, dark body with light legs
11. (2) small, thick, dark body with light legs
12. (1) grooved head, lighter metasoma (dark brown), dark body with light legs
13. (2) antennae setose, "sharp" looking
14. (5) antennae have setae but look soft/fuzzy. smaller
15. (1) venation not very "swoopy", dark

MEGASPILIDAE (CERAPHRONOIDEA):

1. (1) fuzzy/"sharp" pointed flagellomeres
2. (2) fuzzy long-haired flagellomeres

3. (3) flagellomeres long, larger body, dark with lighter legs, BRACHYPTEROUS
4. (1) flagellomeres long, small-bodied, brown, BRACHYPTEROUS
5. (3) large, antennae light at pedicel/radicle, flagellomeres short but widen distally BRACHYPTEROUS
6. (3) large, antennae darker, BRACHYPTEROUS
7. (1) brown, antennae widen distally
8. (2) dark, antennae widen distally
9. (1) flagellomeres long but evenly sized, small, dark body and legs, BRACHYPTEROUS
10. (4) macropterous, dark body and legs
11. (1) macropterous, small, last flagellomere wide/round
12. (1) macropterous, dark, light legs, last flagellomere straight
13. (2) macropterous, large, stigma angular, light legs

CHALCIDOIDEA:

Black mesosoma

1. (1) large, 3 mm, “hunchbacked”, body has pitted appearance, shiny
2. (1) large, 5 mm, black with brown metasoma, brown pigment “stains” on wings
3. (7) setose antennae, longest setae ≥ ½ as long as ant. dark. possible Mymaridae? hindwing stalked
4. (1) dark with dark legs, ~2.5 mm. Huge, flattened antennae
5. (1) black, dark legs, ~3 mm, pitted/setose mesosoma, smooth metasoma
6. (2) ~2.5 mm, large, light legs and antennae. “knobby” antennae. yellow metasomal sternites
7. (1) ~2.5 mm, black/metallic mesosoma, brown metasoma. yellow legs, dark antennae
8. (13) ~ 2 mm, black, shiny, yellow legs, long setae on mesosoma. “bulgy” eyes, “knobby” yellow antennae
9. (1) black with yellow stripe on mesosoma and head, ~ 2.5 mm
10. (1) shiny, black, white legs, huge emarginate eyes, ~ 2 mm
11. (1) large, black, pitted mesosoma, smooth metasoma, yellow/orange legs and wing veins, ~ 3 mm

metallic green/blue mesosoma

…12 through 16: all shiny, green, with marbled brown legs. all have long ovipositors

12. (1) body small, 2 mm, ovipositor 1.5 mm
13. (1) body 3 mm, ovipositor ~ 1 mm
14. (1) body 3 mm, ovipositor ~ 2 mm
15. (1) body 3 mm, ovipositor ~ 3.5 mm
16. (1) body 3 mm, ovipositor ~ 5 mm
17. (1) first metasomal segment narrowed into petiole, ~ 2 mm
18. (2) dark, shiny, white legs, ~ 2 mm
19. (1) dark, shiny, yellow/orange legs, white setae on proterga, long setae on antennae, ~ 2 mm
20. (1) large, black, metallic with orange legs, ~ 2.75 mm
21. (2) same as above but ~ 2 mm
22. (1) green, metallic, bright yellow legs and antennae, ~ 2 mm
23. (1) dark, metallic with yellow legs, stout, ~ 1.5 mm
24. (1) black, metallic, stout, green head, ~ 1.5 mm
25. (1) setose/bristley antennae, long. green mesosoma, brown metasoma, ~ 2 mm

…26 through 37 have black legs…

…..26 through 30 hare larger, 2-2.5 mm. 31-36 are smaller, ~ 1 mm

26. (1) green, long setae on mesosoma, “chunky” antennae
27. (1) green, short setae, antennomeres tight together
28. (1) green, short setae, very thick wing venation

29. (3) blue, short postmarginal vein
30. (1) blue, long postmarginal vein
31. (2) exoskeleton looks thin, antennae with short, light setae. black metasoma
32. (1) stigmal/postmarginal veins thick. bulbous. blue body
33. (1) green, antennomeres tightly connected with bristley setae
34. (1) shriveled, stigmal vein has thick bulge at end, loosely appressed antennomeres
35. (3) shriveled, green, loosely appressed antennomeres, simple venation
36. (1) green/blue, bulgy body, small bulge at stigmal vein but wings glabrous until that point

...37 through 46 have yellow legs

37. (1) large, ~ 3.75 mm, green, yellow scape
38. (1) ~ 3 mm, green/black, large bulge at end of stigmal vein
39. (6) ~ 2 mm, green/blue, large bulge at end of stigmal vein
40. (1) long, ~ 3 mm. dark/metallic. dark pigment "stains" on wings
41. (8) green/blue, ~ 2 mm. "normal" stigmal vein
42. (1) ~ 2.5 mm, pitted mesosoma, tightly appressed antennomeres, "normal" stigmal vein
43. (1) ~ 3 mm? very short, bulgy stigmal vein, long ovispositor (~ 1 mm). (no head)
44. (1) 2.75 mm, green, short ovipositor. short, bulgy stigmal vein
45. (1) ~ 2.5 mm, loosely connected antennomeres, setose mesosoma
46. (3) ~ 2 mm, green, shrivel, light legs

brown mesosoma

...legs totally yellow and/or body has yellow

47. (10) labeled both "Aphelinidae" and "Trichogrammatidae". Small, stout, black with yellow mesosoma and legs
48. (2) yellow face and prosternum. metallic brown metasoma, metallic green mesoterga. dark setae(?) on wings. ~ 2 mm
49. (3) almost vespid-like: yellow mesosoma, yellow and black striped metasoma. knobby antennae. ~ 2 mm
50. (1) dark, large, circle on wing under where stigmal vein should be. yellow and black with a "pointy" metasoma. ~ 5 mm
51. (1) orange and black marbled body, large, ~ 2.5 mm
52. (3) black with yellow legs, ~ 1.75 mm
53. (3) long, setose wings with club at the end (1 enlarged segment). dark with brown legs, ~ 1 mm
54. (1) see above but short setae on wing margin and larger, ~ 2 mm
55. (7) small, brown, with enlarged apical antennomere. setose antennae. Mymaridae
56. (3) ?
57. (16) small, brown, long ovipositor (1/3 body length). Shriveled, short antennae, "normal wings", ~ 1 mm
58. (1) setose wings, LONG antennae, looks like Mymarommatoidea but is Mymaridae
59. (1) small, brown antennae as long as wings, short setae on wings, light face
60. (1) stout, dark with yellow legs, antennae yellow distally
61. (1) small, dark, grey legs, large eyes, long antennae
62. (1) brown, ~ 1.5 mm, bulbous metasoma, short and setose antennae
63. (3) dark with long ovipositor (1/3 body length), ~ 1.5 mm
64. (2) large with brownish wings, dark
65. (31) dark, small, normal venation. May be lumping cryptic species, but lack characters to differentiate

FIGITIDAE (CYNIPOIDEA):

1. (1) Emarginae? brachypterous
2. (1) Anacharitinae

Charipinae
3. (1) brown with yellow legs, ocelli far apart
4. (1) dark with dark legs, ocelli far apart
5. (1) dark with yellow legs but larger than *Figitidae sp.03,* ocelli far apart
6. (3) ocelli close at crown, dark with light legs

Euceroptinae
7. (1) dark with orange legs
8. (1) dark with light yellow/brown legs

Eucoilinae
9. (2) large, dark (male and female?)
10. (2) small, dark, brown legs

BELYTINAE (DIAPRIIDAE, DIAPRIOIDEA):
1. (4) dark with black legs (rest have darker legs)
2. (3) longer ovipositor. brown with light brown tip of metasoma. metasoma looks "pointy". BRACHYPTEROUS
3. (1) smaller than *Belytinae sp.02*, no light metasoma tip
4. (1) small, black, BRACHYPTEROUS
5. (3) large, brown, BRACHYPTEROUS
6. (1) large, black, BRACHYPTEROUS
7. (1) large, brown and orange marbled, long ovipositor
8. (7) black metasoma, large, "bubbly" metasoma (round)
9. (2) black metasoma, large, bubbly metasoma rounder than above
10. (4) black metasoma, dark, setose, orange legs
11. (3) black metasoma, as above but darker and brighter legs
12-18: singletons
19. (23) large, brown, round metasoma
20. (4) pointed metasoma
21-22: singletons
23. (13) small, brown, fully winged, bubbly metasoma
24-26: singletons
27. (2) large, shiny metasoma, brown
28. (4) large, black, setose mesosoma, smooth metasoma
29. (2) brown, setose mesosoma, sparse setae on metasoma
30. (2) black, sparse setae on metasoma
31. (5) very dark, large bubbley metasoma
32-37: singletons
-many males that could not be paired with females, left out of analyses. females tend to have "beady" antennae (ooo) whereas males have longer, thinner antennomeres with sensory apparatus

DIAPRIINAE (DIAPRIOIDEA, DIAPRIINAE):
clubbed antennae
1. (40) antennae: 3 segmented club, brachypterous
2. (15) 3 seg club, brown legs/antennae
3. (1) 3 seg club, brown legs/antennae, excessively large (>3 mm), mouthparts extremely opisthognathous
4. (1) club fused into 1 large segment, small, black
5. (1) 4 segmented "loose" club is just enlarged flagellomeres, dark (black)
6. (19) 3 seg club, lighter yellow/orange/tan legs/antennae

antennae not clubbed
7. (6) excessively large (~4 mm), dark, antennae darker and larger distally

males not included in analyses
8. (3) medium size (~2.5 mm), dark, flagellomeres all equal width
9. (11) *Basalys*, dark body with dark legs, fully winged, straight antennae with male apparatus on segment 4
10. (11) *Basalys*, dark body with lighter legs, fully winged, straight antennae with male apparatus on segment 4
11. (4) *Basalys*, small, brown, setose wings

miscellany
12. (2) dark, lighter legs, brachypterous, flagellomeres gradually widen distally, 2.5 mm
13. (1) as above but ~1.5 mm
14. (2) dark, brown legs, setose wings and antennae (one female and one male). *Entomacis*?
15. (2) straight antennae, brown, setose wings, (male and female?)
16. (1) dark, clear wings, male, knobby antennae (not included in analyses)

BRACONIDAE (ICHNEUMONOIDEA):

Agathidinae:
1. (1) dark coxae, pigmented areolet
2. (2) orange coxae, areolet unpigmented distally

Rogadinae:
1. (1) metasoma entirely orange, small, light setae
2. (2) metasoma outlined in black, many standing setae

Hormiinae:
large body (>2 mm):
1. (1) stocky body
2. (2) slender body, unpigmented vein closing 2° submarginal cell distally

small body (<2 mm)
3. (1) brown (no wings? may have been lost?)
4. (1) black (winged)

Braconinae:
1. (1) ≥ 4 mm
2. (1) 2-3 mm
3. (2) ~2 mm

Aphidiinae:
see venation image for 1-5:
1. (1) all dark
2. (2) orange legs, broad head, facial setae, small
3. (1) small, 9 flagellomeres, smooth
4. (2) black with brown legs, “sharp” or serrate looking antennae, many flagellomeres
5. (1) “large”, dark with orange ventrites/legs/coxae/pleurites ventrally
6. (1) “normal” venation
7. (1) very dark, less venation

Cheloninae:

1. (1) black femur, black antennae, larger
2. (1) brown/tortoiseshell legs/antennae

Microgastrinae:

1. (1) large, dark with brown/orange legs
2. (1) mesopleurite smooth/shiny/bluish refulgence
3. (1) mesopleurite rough with setae over all except dorsal/center

Homolobinae: (*Charmon*?)

1. (1) larger, shiny, smoother?
2. (1) slightly smaller, "duller", hairier mesosoma dorsally

Braconidae: (no subfamily designation)

(1) UNK- no head

stout black body with orange legs:

1. (1) small, reduced/unpigmented wing venation, short antennae
2. (1) closed cell after stigma
3. (1) hard looking, not as above

4. (1) small, round head
5. (1) reduced wing pigmentation/"bleeding", black with orange legs
6. (1) similar to Hormiinae in that 2° submarginal cell closed distally but all black
7. (1) twisted mandibles, brown, >3 mm

Alysiinae:

"thick stigmal vein"

1. (1) *very* thick stigma vein, ¼ wing width
2. (1) brown body, tan legs
3. (9) black body, tan/orange legs

4. (8) "small blacks"

"small browns"

5. (11) ~2 mm
6. (8) ~1 mm

"generics" (medium-sized)

7. (12) dark mesosoma, lighter metasoma, >3 mm
8. (7) dark mesosoma *and* metasoma, >3 mm

"miscellany"

9. (2) Alysiine-like but triangular stigma. Large, brown
10. (1) stigma massively swollen. large. black mesosoma, orange/black metasoma
11. (2) large, super long antennae, triangular stigma
12. (2) large triangular stigma, shiny, orange legs, >2 mm
13. (1) large triangular stigma, brown, >2 mm, ovipositor as long as body

ICHNEUMONIDAE (ICHNEUMONOIDEA):

extra large-bodied (>10 mm)

1. (1) "stereotypical" ichneumonid, orange, setose
2. (1) black and yellow, metallic shiny setae, large hind coxae

3. (1) black with orange coxae and legs, meta tibia/tarsi black
4. (1) Tersilochinae- black with brown legs
5. (1) Tersilochinae- black, brown legs and metasoma center
6. (1) black and brown/orange marbled, antennae white in middle
7. (2) apterous Cryptinae, dark with light legs, slender
8. (1) apterous Cryptinae, small, very dark
9. (4) apterous Cryptinae, tortoiseshell color, marbled, slender
10. (7) apterous Cryptinae, large, brown, "curvy", body >2 mm
11. (3) apterous Cryptinae, small, brown, "curvy", body ≤2 mm
12. (1) brachypterous, large (~1 cm), brown/black, slender
13. (1) brachypterous, large but stout, antennae white in middle
14. (1) exodont mandibles, similar to Alysiine but has "horsehead" cell

large-bodied (>5 mm)
15. (2) dark with brown metasoma, antennae on a shelf
16. (2) short ovipositor, black mesosoma, brown metasoma with black posterior
17. (3) long ovipositor, black mesosoma, brown metasoma with black posterior
18. (2) shiny, dark, almost bluish refulgence. long antennae. white/brown striped legs. white around wing attachments
19. (1) same as above but less white, especially where wing connects
20. (1) see above but smaller
21. (1) long ovipositor, dark with brown marbling, open areolet
22. (1) dark with brown apically. closed areolet
23. (1) dark with brown stripes on metasoma. open areolet

medium-bodied (~5 mm)
24. (3) shiny, dark brown with lighter legs and antennae. antennae short.
25. (6) dark with light legs. long antennae. "rectangular" areolet. large stigma
26. (1) above but dark legs
27. (1) dark, shiny with white around wing attachments. two white adjacent scutellum
28. (1) same as above but whole scutellum is white
29. (1) same as above but not white quite to top of scutellum
30. (1) pale face, orange/white/brown striped legs. open areolet
31. (2) dark, stout, brown legs, fat flagellomeres
32-67. singletons

small-bodied (<5 mm)
yellow on face:
68. (1) yellow anteriorly, black on sides of eyes, short antennae
69. (1) yellow around eyes and anteriorly, long antennae
70. (2) dark with light legs, long antennae on shelf. shelf is light. dark stigma
71. (2) same as above but light stigma
72. (1) yellow around eyes but dark top of head
73. (1) yellow mandibles and just above clypeus. long, dark antennae
74. (1) marbled face. long, thin antennae
75. (1) marbled face. long, thick antennae. larger than *Ichneumonidae sp.074*
76. (2) light face, dark body, wing with sharp curved vein after stigma
shelf face with beady antennae:
77. (9) grey eyes, dark dorsally, lighter legs and anterior face
78. (1) as above but light/white/pink? eyes
date may-june
79. (1) all black, same sharp vein curve in wing after stigma as in *Ichneumonidae sp.076*
80. (2) light legs short antennae with long flagellomeres, dark body
81. (2) shrivel, lighter ventrally, sharp vein curve in wing after stigma
82. (2) same as above but darker and larger
83. (1) dark with orange legs. large. shorter antennae

84. (1) small, shriveled, reduced venation
85. (3) shiny, open areolet, more normal venation, light legs, dark body
86. (5) as above but larger
87. (1) as above but larger and yellow/brighter legs
88. (2) small, dark, shriveled, light spot on face
89. (2) as above but no light spot on face
90-95. singletons
date july-august
96. (3) dark, large eyes, metasoma black-brown-black
97. (3) dark with yellow legs, shiny, sleek, thin, open? areolet
98. (2) dark, shiny with yellow legs, can't get wings to furl open
99-124. singletons

SCELIONIDAE (PLATYGASTROIDEA):

Telenominae:

1. (50) *Dissolcus*. Males have straight antennae, female have clubbed (I think). 3rd flagellomere has curved sensory apparatus that male diapriids have, suggesting they may be males of same morphospecies
2. (5) *Trissolcus*. smaller than *Dissolcus*
3. (1) huge, bulgy mesosoma. undersize metasoma
4. (1) possible *Platytelenomus* sp.

Scelioninae:

1. (57) *Gryon*. clubbed antennae (except male?). xanthic
2. (16) *Idris*? clubbed antennae (except male?) dark but have lighter 1st metasomal tergite
3. (2) brown, "large" (1 mm) (robust). antennal segs tightly spaced
4. (1) *Spinteleia*? wings small but still reach mid metasoma, black
5. (1) full wings, black
6. (1) full wings, black with orange legs, large
7. (2) brachypterous, brown, small, (male and female?)
8. (6) brachypterous, black

Teleasinae:

1. (87) brown, brown legs, brachypterous (or apterous), 6 seg clava
   -male- winged. antennae without club and long/setose. Flagellomere 3 has sensory apparatus. See drawing of genitals
2. (23) as above but yellow legs (pale)
3. (12) black, brachypterous, female
4. (2) small, brown, brachypterous, small eyes, female
5. (1) small, brown, full wings, pale legs, not clubbed antennae, female
6. (21) small, black, full wings
7. (9) large, black, full wings
8. (1) dark, large, setose wings

-5 unique males unmatched to females, not included in analyses

3 misc. unidentified scelionidae

PLATYGASTRIDAE (PLATYGASTROIDEA):

1. (5) brown, pale legs, large, no venation
2. (1) smaller, dark, no venation
3. (1) larger, dark, lighter legs distally, no venation

4. (1) dark, setose petiole, no venation, large eyes pointy scutellum
5. (1) large, brown, round scutellum
6. (1) small, black, rounded/triangular scutellum. (no head).
7. (1) very large, dark
8. (2)

-17 misc unidentified platygastroidea. not identified. not included in analyses.

PROCTOTRUPIDAE (PROCTOTRUPOIDEA):

1. (1) dark with dark legs (male)
2. (2) dark with orange legs (male and female)